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THE

NATURAL HISTORY OF PLANTS

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THE

NATURAL HISTORY OF PLANTS

THEIR FORMS, GROWTH, REPRODUCTION, AND DISTRIBUTION

FROM THE GERMAN OF

ANTON KERNER VON MARILAUN
PROFESSOR OF BOTANY IN THE UNIVERSITY OF VIENNA

TRANSLATED AND EDITED
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WITH THE ASSISTANCE OF
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WITH ABOUT 2000 ORIGINAL WOODCUT ILLUSTRATIONS AND SIXTEEN PLATES IN COLOURS

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EDITOR'S PREFATORY NOTE.

With this, the second and concluding volume of *The Natural History of Plants*, a brief statement and explanation of my position as editor is imperative. As stated in my note to Volume I. the English text there followed that of the original with considerable fidelity. In the second volume I have less consistently followed this course. Throughout I have not hesitated to add or substitute new matter, though no overt indication of such departure from the original is given either by different type or otherwise. It is needless to explain that these changes are only such as the advance of botanical knowledge has rendered necessary since the original was written, and that I have never desired to depart from the intention of the author. To the specialist these modifications will be from time to time apparent; the general reader will perhaps treat me with indulgence should he think that in this matter my judgment has been at fault. Though changes occur throughout the volume, I have preserved intact the main conclusions of the author and the facts upon which they are based. To have altered these in any way, even had I been so minded, would have been inconsistent with the duties of an editor and translator. But in the purely systematic portion of the work I have been restrained by no such scruples. Professor Kerner himself regarded that portion of his work as but tentative, and as it was difficult to merely modify, the whole of this portion has been written *de novo*, from the Thallophytes to the end of the Gymnosperms (pp. 616–728), and in part the Monocotyledons. The exigencies of the serial issue of *The Natural History of Plants* alone has prevented the re-cast of the Dicotyledons, which stand with little modification as in the original. For the portion dealing with the class *Gamophyceæ* up to the end of the *Conjugatæ* (pp. 627–659), I am indebted to my colleague, Mr. A. G. Tansley of University College, who has devoted considerable attention to the group in question. To him I now offer my hearty thanks. The glossary of botanical terms makes claim neither to completeness nor originality. Though a large number of the definitions and explanations have been written specially for this book, I have never hesitated to lay published sources under contribution. The laborious task of constructing the index has fallen to Mr. George Brebner, and to him is due the gratitude of such as gain through it direct and ready access to the body of the work.

F. W. O.

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THE HISTORY OF PLANTS

THE

NATURAL HISTORY OF PLANTS.

INTRODUCTION.

Sources of a History of Plants.—The Language of Botanists.

SOURCES OF A HISTORY OF PLANTS.

FROM the sixteenth to the latter part of the eighteenth century, "Historia plantarum" was the customary title for botanical works. Most of the scholars of that time took as their authorities and models the writings of Theophrastus, the celebrated pupil of Aristotle, together with the thirty-seven books constituting Pliny's "Historia naturalis". Thus it came about that the titles of the new books were similar to those of Theophrastus and Pliny. However, all these books are anything but histories of plants, if in the idea of a history we include an account of the changes which occur within the limits of space and time. In reality the bulky folios of Clusius, Bauhin, and Haller, the title-pages of which bear the inscription "Historia plantarum", contain descriptions merely of the external characters of plants, accompanied by only sparing details of the situations in which these plants had been found growing wild. Works of this kind, dealing with limited areas of country, were later on distinguished by the name of Floras. By this name they are still known.

Although the authors of the Flora had no such purpose in view, their works furnished the starting-point for a real history of the vegetable world. A comparison of the Floras of neighbouring regions shows that certain plants inhabit a greater, others a lesser area; that the boundaries of the species confined to a distinct district coincide with territories inhabited by various races of mankind; that the boundaries of this and that species coincide and stand in relation to various climatic and other conditions.

All plants have the power of propagating themselves. They send their offspring forth as colonists towards all points of the compass, and endeavour in this way to enlarge their areas of distribution. Suppose that a species hitherto subsisting in localities where there are seven months of snow and five months of vegetation in the year multiplies, and that its descendants are scattered in all directions, what would happen if any of these emissaries reached places where frost and snow prevail for eight months instead of seven, and where the season for vegetation is confined to four months? They would succumb to the inhospitality of the climate; and it follows that a limit to the distribution of the species in question would be attained at a line connecting all places which possess a climate of equal rigour. This does not preclude the possibility of other causes constituting a barrier to the distribution of the same species in other directions. Peculiarities of soil, for instance, may prevent the naturalization of a plant; or, its spread may be baffled by the opposition of plants already long settled in the place invaded; or any other like impediment may operate as a check. Facts of this kind, being brought to light by the comparison of different Floras, led to detailed research into the means of reproduction and distribution in plants, to a study of the many contrivances for their propagation, and of the nature of the equipments which enable the descendants of a stock to enlarge the area where it grows.

Side by side with these investigations into the history of individual kinds of plants, there was developed a special department of research with the view of determining the actually-existing boundary-lines of distribution — the so-called lines of vegetation—of particular species, and of ascertaining all the conditions of soil and climate affecting plant-life which prevail along these lines, so as to take into consideration all the possible causes of limits to distribution. The range of observations was likewise extended to displacements of the lines of vegetation, to the advance of particular species in one direction or another, and the suppression and annihilation of others within historic times; thus a chronicle of plant migration was started.

The unlooked-for discovery of the multitude of plants which flourished upon the earth ages ago, and have been preserved as fossils, led to a further comparison of forms—viz. of those now living with those that have perished. There was no evading the idea that existing species are derived from others now extinct; on the contrary it proved so attractive that it was followed up with the greatest interest and zeal. Then these inquiries into the parentage of species naturally led further to the whole problem of their origin—in short, to a study of the history of species.

The range of vision continued to become yet wider. It is impossible that the dwarf willows and birches found living in Greenland at the present day should be descendants of the maples and beeches which grew there in the Tertiary Period, or that the alders or pines now flourishing on the soil above the beds of bituminous coal at Häring in Tyrol should have sprung from the Proteaceæ and Myrtaceæ which formerly covered the same ground, as we learn from the fossil remains found there. Local changes must have taken place, and the various floras must have undergone a process of expatriation on a large scale not unlike that of men at the time of the migration of tribes. New realms were then occupied by those floras in a manner corresponding to the formation of states by the struggling and mingling races and nations of mankind. The knowledge of the fact that a plant's form depends at the present day upon soil and climate entitles us, moreover, to infer that a similar connection existed in past times between the forms of plants and their conditions of life, and enables us to discover what gave rise to migrations and caused the redistribution of floras. These phenomena are the subject-matter of the History of the Plant World in the fullest meaning of the phrase; and their explanation is eagerly sought by modern botanists.

In 1853 Unger, to whom all branches of Botany were equally familiar, made the first attempt at such a history of plants. Since then a great number of new discoveries have been made both in the Old World and the New. Men with minds intent upon this object are everywhere searching for the fossil remains which throw such valuable light upon it; but, so far, this—the most recent branch of Botany—has not led to a comprehensive result. We find ourselves, as it were, in the midst of a stream in full flood owing to the number and magnitude of its tributaries, and it is no easy matter to steer clear of shoals and run safely into harbour. Some decades hence it may perhaps be possible to write an accurate and complete history of the plant world founded upon the mass of authentic evidence which will by that time have been winnowed from the records of past ages. At present I must content myself with sketching in general, and often ill-defined, outline the changes which take place in the world of plants.

The foregoing introductory remarks concerning the sources from which materials for a history of plants are derived serve also to explain the arrangement of the subject-matter to be dealt with in the Second Volume of this work. The order of presentation of the different parts of the subject will follow the stages of development of the science. A history of the entire plant-world considered as a single great community must be preceded by a history of species. But each species is the sum of numberless individuals, which are alike in constitution and have the same external characteristics, and a history of species therefore presupposes a knowledge of the history of the individual. Accordingly, our first business is to describe the rejuvenescence, multiplication, and distribution of individuals, and to show by what means a plant, considered as a separate organism, maintains itself, takes possession of its habitat, and is enabled to keep its hold on that habitat up to the moment when it is replaced by descendants endowed with a vitality of their own.

THE LANGUAGE OF BOTANISTS.

Before entering upon a description of any of the above phenomena, I feel it necessary to say a few words respecting the technical botanical terms of which I shall make use. The need of short and compendious names to denote particular forms, particular organs, and particular processes, has been always universally recognized, and more or less appropriate additions to our vocabulary have been made by men of science from time to time. As might be expected, these designations are not only an expression of the particular standpoint to which, at the time of their invention, the actual knowledge of plant-life had most recently attained; but they are also liable to bear the stamp of theories advanced by eminent naturalists of the day, or of the hypotheses which happened to be then in vogue. The progress of true knowledge is too often hindered by the fact that men exalt their speculative theories to the position of "laws of nature", and when they first encounter contradictory evidence twist and turn it until it appears actually to verify those theories. We need not inquire in these instances how much is due to self-deception and how much to prejudice and dogmatism on the part of the investigators. Certain it is that such a perverse method of research, especially when supported by the authorized beliefs of the thoughtless multitude, acts as a drag on true science. Fortunately, however, it is nothing worse than a drag. For, sooner or later, the conviction again asserts itself that our notions respecting the history of plants must be derived from the facts observed in their entirety and purity, instead of facts being made to fit a preconceived opinion—some being explained away as exceptions, whilst others are altogether ignored and suppressed.

In all sciences for which it is requisite to invent technical terms—and in Botany no less than in others—we find that the terminology bears traces of ideas formed at earlier periods, and now rejected as being based on insufficient experiment or imperfect observation, on self-deception or prejudice, as the case may be. The question has, therefore, repeatedly been raised whether it is better to retain such names and modes of expression, although they are likely to suggest wrong ideas to students, or to abolish them and substitute new ones in their stead. There are strong arguments for both courses. The chief advantage of retaining the old terms is that readers of modern works are thereby enabled to understand more easily the writings of older botanists. We have also to consider the probability that in rejecting old terms and inventing new ones we may fall into the same errors as our predecessors. Any one who has worked in the field of Botany for more than forty years, as I have done, must have found that on an average every ten years prevailing ideas have undergone a change. He has seen how theories, which for a time influenced every branch of the science, and were actually standard conceptions in many departments of research, have sooner or later had to give place to new ones. He knows how often a naturalist is compelled, in consequence of fresh and unexpected discoveries, to let go a position which he has considered impregnable, and which has become endeared to him by long familiarity. Thus, experience teaches diffidence, and one learns to attribute only a temporary value, so to speak, even to one's own original theories, and to rest assured that, in a few decades, what now appears to be nearest the truth will be superseded by something else which comes still nearer to it.

But if, whenever a fresh stage of knowledge were reached, all terms and phrases which had become antiquated and no longer quite applicable were abandoned and replaced by others, and if in addition new names were introduced corresponding to every modification in the results obtained by observing all the different processes and appearances with which we have to deal, our science would inevitably be rendered far less accessible—and this consequence would be much to be regretted. However strong the desire to understand the secrets of plant-life, it could only be satisfied at the cost of learning a special scientific language; and Botany would become, in an even greater degree than is the case at present, a close study for specialists, instead of being the common property of the many inquiring minds to whom the results of our researches by right belong.

Accordingly, we shall retain so far as is practicable the recognized scientific terms. Where they are no longer quite suitable they will be briefly elucidated; and, when the conceptions to which they refer have been expanded or limited, the old established names will also be taken in a wider or a narrower sense as the case may be. New expressions will only be introduced where their use is productive of greater clearness and distinctness in the ideas involved; and even these additions must be in harmony with the terms already in existence.

It is worthy of note too that many foreign words, which have been longest established and also subject to frequent use by botanists, originally meant something altogether different from what they are intended to denote at the present day. In the very first section of this volume a whole series of such words will be employed. The history of the plant-individual is there dealt with. What is an "individual"? The word comes from *dividere*, to divide, and denoted originally a thing which is not divisible. But there is no such thing as an indivisible plant. The survival of plants, their reproduction and multiplication, are all dependent on processes of division; and any species whose individuals were not divisible, would be doomed to inevitable destruction. The characteristic property of an individual cannot therefore lie in absolute indivisibility. A qualification has in consequence been inserted in the definition, and an individual is explained to be a thing which cannot be divided without ceasing to be, as heretofore, an organized being subsisting independently, in which each single part belong indispensably to the whole. Even this definition is not appropriate to a plant. The living protoplast of a unicellular plant—an organism which must without question be conceived as an individual—divides into two halves, which separate from one another and constitute two independent individuals. This instance affords, however, an indication of the true definition. A plant-individual is an organism which can and does live independently and without the aid of other organisms of the same form. There are plant-individuals each of which consists of a single protoplast, whilst others are composed of many protoplasts living together. In the latter there is for the most part a division of labour accompanied by a corresponding variety in the forms of the different parts of the individual; but even in these cases individuality is not necessarily destroyed by division. Where division of labour has been carried so far as it is in a plant provided with stem and leaves (*cf.* vol. i. p. 584), it used to be thought necessary to look upon the structure as an association of individuals. Each single shoot was conceived to be an individual because it possessed the power of continuing to live after it had been separated from the axis, and on that assumption each one of the higher plants was built up of such and such a number of separate individuals. Later on, however, inasmuch as every branch of a shoot is capable of living when separated from the rest and of producing a new independent plant, the parts of a shoot came to be considered as being individuals, and the term "Anaphytes" was applied to them. We shall see hereafter the extent to which this conception is of importance in relation to the subject of alternation of generations. It would be out of place to treat it more fully at present.

Another conception of the plant-individual must also be mentioned here. When the impossibility of defining it as indivisible was recognized, the strange expedient was invented of assuming the existence of divisible individuals and of representing all parts which have been produced asexually and have become independent as belonging to a single individual. A potato puts forth thirty or forty fresh tubers in the course of a few years, and all these were considered as collectively constituting one single individual, as also were the countless young carnation-plants which are to be derived by means of cuttings from one old plant. The general rule was that only an organism produced by sexual process was to pass as an individual. Cuttings, tubers, and the like, detached from such an organism would be, according to this conception, merely parts of one individual, even though they were capable of living quite independently and at a distance from one another.

This definition, the invention of philosophers, has never been taken seriously by naturalists, and I only cite it because it introduces another important problem which I purpose to treat in an exhaustive manner in the first three sections of this volume, namely, the question of the propagation or generation of plants. The modes of reproduction in plants have been subjected in recent times to most patient investigation on the part of botanists gifted with the keenest powers of observation, and their researches have led to the conclusion that in most—probably in all—divisions of the vegetable kingdom two kinds of propagation occur. In each case a single protoplast forms the starting-point for the new individual; but, in the one, this protoplast does not require the special stimulus afforded by union with another protoplast, whereas, in the other, in order that a new individual organism may be produced, a pairing—*i.e.* a union of the substances—of two protoplasts, which have come into being at different spots, must take place. The former is called *asexual* reproduction, the latter *sexual* reproduction. All reproductive bodies arising asexually are included under the name of *brood-bodies,* whilst those which are associated with the sexual process may be termed broadly *fruits.*

There are all grades of brood-bodies, from the single cell to the completely formed plant. Brood-bodies, if unicellular, are termed *spores,* if multicellular, *thallidia*; and those which constitute rudimentary shoots are called *buds.* The bud form of brood-body either detaches itself from the living parent-plant, or else, as more frequently happens, it becomes independent through the death of the plant from which it sprang. In the latter case the off-shoots remain in the immediate vicinity of the parent-plant. In the case of trees and shrubs the buds do not sever themselves from the axis on which they were developed, but continue their connection with it as they grow into shoots, and in this manner are formed those compound individuals to which reference has been already made. It is much less common for full-grown shoots to detach themselves from the parent-plant and act as brood-bodies.

Fruits of all degrees of complexity are also found. They are sometimes single cells, sometimes groups of cells, and sometimes complete plants in miniature. Usually the fruit—or at least the most important part of it which contains the fertilized ovum or the embryo produced thereby—becomes detached, when ripe, from the parent-plant; but, in many groups of the vegetable kingdom, in Ferns, Mosses, Lichens, and Florideæ, for example, the fruit remains at its place of origin and preserves its connection with the mother-plant whilst itself developing into a new generation, which, however, does not produce fruits but spores. When asexual and sexual reproduction take place alternately in a definite manner, we speak of an *Alternation of Generations.* Hitherto the subjects of fruit-formation and of the alternation of generations in their relation to the History of Plants have remained unrecognized and unelucidated. In one of the following sections of this volume an attempt will be made to solve this great mystery.

THE GENESIS OF PLANT-OFFSPRING.

1. ASEXUAL REPRODUCTION.

Spores and Thallidia.—Buds on Roots.—Buds on Stems.—Buds on Leaves.

SPORES AND THALLIDIA.

In the chapters on ferns in the old herbals, attention is invariably directed to the extraordinary phenomenon that the plants in question do not produce flowers or fruit, and yet propagate their kind and multiply abundantly, and the remark is made that these plants will often spring up quite unexpectedly in caves, or in the cracks of old walls, without any seeds having been previously perceptible there. Hence in Germany a fabulous story was invented that the seeds of ferns were formed in a mysterious manner at the time of the summer solstice only, and that these seeds could only be collected on Midsummer Eve by persons initiated in the mystery who made use of certain magic words on the occasion. Hieronymus Bock or Tragus, as he called himself in accordance with the then prevailing fashion of translating names into Greek, preacher and physician at Hornbach in 1532, was the first to contradict this childish superstition, and to convince himself of the possibility of obtaining "fern-seeds" without the use of incantations. In his Herbal, published in 1539, he gives the following account, which is in many respects interesting, of his endeavours to collect the seeds of ferns: "All our teachers write that the fern bears neither flower nor seed; nevertheless, I have four times looked for the seed in the night of Midsummer Eve, and have found early in the morning before daybreak small black seeds like poppy-seeds on cloths and on the broad leaves of mullein beneath the stems in varying quantities. . . . I have used no charm or spell in this matter, but have looked for the seeds without any superstition and have found them. One year, however, I found more than another, and I have sometimes been out without success. I have not gone alone to fetch the seeds, but have taken two others with me, and have made a great fire in an unfrequented spot and let it burn all through the night. How the thing came to pass, and what secret nature intends to reveal by it, I cannot tell. I have stated all this because all our teachers describe the fern as being without seeds."

There can be no doubt that by the brown seeds Hieronymus Bock meant those structures which, about two centuries later, were named "spores" by Linnæus. But even in the time of Linnæus the whole subject of spores, especially in their relation to fruit, was shrouded in complete obscurity. The word "spore" is derived from the Greek, and signifies etymologically precisely the same as "seed", and spores were considered to be peculiar seeds, formed by means of some mysterious processes of fructification. As late as fifty years ago the spore was defined as "that part of a cryptogamic plant which corresponds to the seed, and from which, although it contains no germ, a new plant can be developed".

The mode of fructification in the Fern, and, in general, the entire history of its development, were discovered for the first time in 1848. It was then shown that these plants pass through two kinds of regularly alternating generations. One of these is itself inconspicuous, but bears reproductive organs and produces fruits; the other, springing from the fruit, which continues its connection with the parent-plant, is distinguished by fronds and produces spores. Thus the fronds of Ferns bear no sexual reproductive organs, and the spores formed upon them cannot therefore be looked upon as fruits or even as seeds, a seed being part of a fruit.

Some people, it is true, treat the entire frond-bearing Fern-plant as a fruit and the spores on the fronds as part of this fruit, although such a theory involves the admission that fruits may strike root, multiply by means of runners and continue to grow for many years, putting forth annually new spore-bearing fronds. According to this view, which I cannot endorse, a gigantic tree-fern, aged a hundred years, would be a fruit, and to be consistent it would be necessary to regard a whole grove of Horse-tails as belonging to one single fruit. Other botanists, whilst denying that the Fern-plant with its roots and fronds is the fruit itself, are yet of opinion that the formation of spores in the Fern is a consequence of the process of fruiting, inasmuch as the Fern-plant would never make its appearance at all but for the formation of fruit by the previous generation; and they hold that the spores of Ferns, and of their allies the Horse-tails and Club-mosses, should on that account be distinguished from those of other Cryptogams. To this view there are two objections. In the first place, we know many cases wherein a Fern-plant with spore-bearing fronds is developed from the first generation without any formation of fruit having taken place, and the plant in these instances is in no way different from those which have sprung from fruits of the first generation. Secondly, it is difficult to see why the sporogenous generation should be more dependent on the fruit of the first generation in the case of Ferns than in many other Cryptogams, which similarly exhibit an alternation of generations.

As the spores of Ferns, and of Cryptogams in general, are not the direct result of a process of fertilization, they are not parts of fruit, but are brood-bodies. They should be placed by the side of the bud forms of brood-body presently to be described, though differing from these in that they always produce a single layer (*i.e.* a thallus) only, and never a leafy, axial structure. They are just as characteristic of Cryptogams as buds are of Phanerogams or Flowering Plants, and as the name of Cryptogam is no longer quite appropriate, it is often replaced by the term "sporogenous plant". Before the discovery of the alternation of generations in Cryptogams, the name spore was applied to many fruits and rudiments of fruits, particularly where these happened to be unicellular, an error which we should be careful to avoid at the present day. When we come to the description of fruits and their origin, we shall have occasion to return again to this subject.

The places where spores originate are remarkably varied. In some plants nests of cells make their appearance in the interior of an extensive tissue; in others single cells are exposed on the surface. The task of spore-development devolves sometimes upon a part of a green stem or leaflet. Sometimes—in plants devoid of chlorophyll—upon the protoplasmic contents of a tubular structure, and sometimes upon the abstricted ends of hyphal filaments. The best way to arrive at an idea of the extreme diversity in this respect is to classify spores in groups according to their mode of origin.

One group comprises all such spores as are formed in the cells of a tissue. Amongst these are the spores of Ferns, Rhizocarps, Horse-tails, Club-mosses, and the numerous kinds of Mosses and Liverworts. In one sub-group of Ferns papillæ spring singly from the epidermis clothing the ribs of the fronds, each papilla being divided by a transverse wall into a free extremity and a stalk-cell. Both cells of the papilla become partitioned so as to form bodies of tissue, and the one that developes from the free terminal cell assumes an oval or spherical shape. In this latter ball of tissue a tetrahedral central cell and an envelope composed of several layers of cells may be distinguished. By internal partition of the central cell a little cluster of cells is formed, whilst, in the meantime, the inner layer of cells composing the envelope is dissolved, so that the whole now assumes the aspect of a receptacle inclosing a ball of cells embedded in a fluid matrix. Each cell of the cluster next divides into four compartments, and the protoplasts which constitute the contents of these chambers provide themselves with membranes and become disconnected upon the solution of the framework of their home. These separated cells are the spores. To the naked eye they have the appearance of a powdery mass. As has been said, of the cell-layers which formed the envelope of the sporogenous tissue, only the inner one was dissolved; the outer layer persists and constitutes a kind of capsule, to which the name of spore-case or "sporangium" is applied (see figs. 189 [13], 189 [14], 189 [15]). A collection of sporangia of this sort is called a "sorus". In the Polypodiaceæ—a family of Ferns to which the majority of European species belong—the sori may be seen on the backs of the fronds (see 189 [5]). Upon the veins running through the green tissue are seated little cushion-like groups of cells. Each cell in one of these cushions is capable of developing into a stalked sporangium, and sometimes a single sorus consists of no less than fifty such stalked sporangia. In the Cyatheaceæ also, which include most of the Tree-ferns, the sori are developed on the under side of the fronds, but in their case each is borne on a kind of peg projecting at right angles to the surface of the frond. The sporangia derived from the epidermal cells of this peg are very shortly stalked. An annular wall is produced from the green tissue of the frond and surrounds the sporangiferous peg, which consequently stands up from the middle of a cup (see figs. 189 [10], 189 [11], 189 [12]).

In the delicate and graceful Hymenophyllaceæ—Ferns with a resemblance to

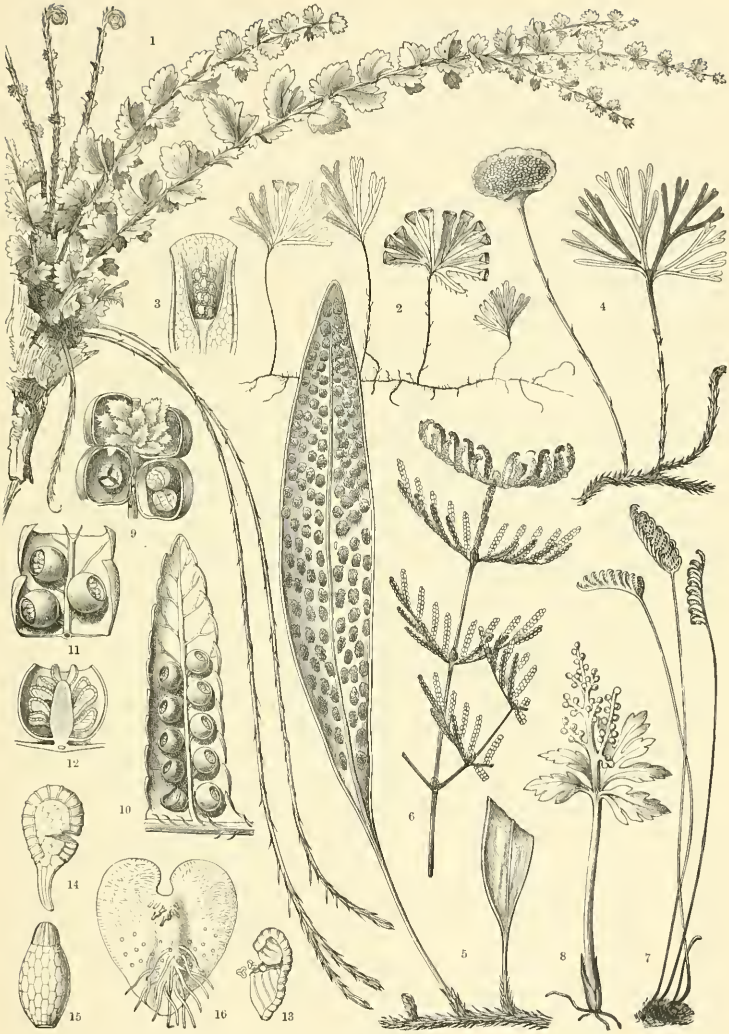

Fig. 189.—Ferns.

Nephrolepis Duffi. [2] *Trichomanes Lyelli.* [3] Sorus of the same Fern with cup-shaped investment seen in longitudinal section. [4] *Rhipidopteris peltata.* [5] *Polypodium serpens.* [6] Pinna of *Gleichenia alpina.* [7] *Schizæa fistulosa.* [8] *Botrychium lanceolatum.* [9] Under side of a pinna of *Gleichenia alpina*; in the two upper cavities the sporangia are covered by leaflets, in the under ones they are exposed. [10], [11] Pinna of *Cyathea elegans.* [12] Longitudinal section through a Sorus and Cup of *Cyathea.* [13] Sporangium of *Cyathea.* [14] Sporangium of *Polypodium.* [15] Sporangium of *Schizæa.* [16] Under side of the Prothallium of Spleenwort. [1], [2], [4], [5], [6], [7], [8] natural size; [3], [9], [10], [11], [12], [13], [14], [15], [16] magnified from 5 to 20 times.

Mosses, and belonging for the most part to tropical regions—the veins of the pinnæ project beyond the margin of the green tissue and form styloid processes whose epidermal cells become the points of origin of sporangia. Each styloid process thus constitutes an axis bearing the sporangia, and the entire sorus has the form of a little spike. But the sorus itself stands in a cup formed by an upgrowth of the green tissue at the margin of the pinna (see figs. 189 2 and 189 3).

In the three groups of Ferns above dealt with the sporangia arise from epidermal cells. In the Gleicheniaceæ and Schizæaceæ (two specimens of which are shown in figs. 189 6 and 189 7) the sporangia are modified leaflets. We must here remark that the fronds of Ferns in spite of their similarity to foliage-leaves are not to be regarded as such, but as phylloclades, whilst the scales upon the fronds must be considered to be leaves. We shall refer to this again later on. Now, in Gleicheniaceæ and Schizæaceæ some of these small scaly leaves are metamorphosed into sporangia which here take the form of rounded bodies set in rows of pit-like cavities hollowed out of the pinnæ, whilst other scales constitute protective coverings to these sporangia. The relation existing between the various parts in the case of a pinna of *Gleichenia alpina* is shown very clearly on an enlarged scale in fig. 189 9.

In respect of origin and development the spores and sporangia are again quite different in the group of Ferns comprised under the name of Ophioglosseæ, one species of which—viz. the spear-shaped Moonwort (*Botrychium lanceolatum*)—is represented in fig. 189 8. In these Ferns, the sporogenous portions take the form of nests of cells embedded in the tissue of the frond. The cells in these niduses become partitioned each into four chambers, and the latter contain protoplasts, which surround themselves with membranes and become spores. The spores are set at liberty as a consequence of the solution of the walls of the chambers, and they occupy, in the form of a fine powder, little vesicular cavities in the tissue of the pinnules. The epidermis of these pinnules now serves as the wall of the cavities, *i.e.* of the sporangia.

Each plant in the group of the Ophioglosseæ exhibits two kinds of frond: the one kind develops no spores and has the appearance of a green foliage-leaf; the other produces sporangia, which are arranged either like bunches of grapes or in spikes consisting almost entirely of the sporangia (see fig. 189 8). A similar arrangement may be observed also in many Ferns belonging to other divisions, as, for instance, in the genera *Allosorus*, *Struthiopteris*, and *Blechnum*, representatives of which occur in the European Flora as well as in others. In other cases, such as the Flowering Fern (*Osmunda regalis*), for example, sporangia are only formed on the upper portion of a frond, whilst the lower segments are foliaceous. A very peculiar form is that of *Rhipidopteris peltata*, a fern indigenous in the mountainous regions of Mexico (see fig. 189 4). Besides the flat, fan-shaped fronds which produce no sporangia, other fronds shaped like funnels or shallow bowls are developed, and the spore-cases are produced from the epidermal cells in the hollows of these fronds.

In the last case it is worthy of note that the sporangia are formed on the upper surface of the frond, for this is of very uncommon occurrence. They are usually situated on the under surface of the frond, the reason being that they are thus best sheltered from both rain and sun. Most instances exhibit in addition a further safeguard against excessive moisture or desiccation in the form of a special awning covering the sporangia. This awning is either an outgrowth from the cells forming the apex of the sporangiferous cushion or peg, and takes the form of a delicate membrane stretched over the whole sorus and known as an *indusium*, as in our male Shield Fern (*Aspidium Filix-mas*), or else small, scale-like leaflets spread themselves over the sporangia, as in the Gleichenias (fig. 189 [9]), to which reference has already been made, and in the no less remarkable Lygodiums and Davallias. Sometimes five or six squamous leaflets stand in a circle round the sporangia and envelope them so that the whole looks deceptively like a closed flower, as in the genera *Schizocæna, Hymenocystis,* and *Diacalpe*; or, these leaflets form a sort of box, which opens with a lid, as in *Cibotium*. In other cases, again, membranous bands or borders grow up from the surface of the frond, and the sporangia, which are arranged in a long line, are covered over by them, as occurs in *Lindsaya* and *Blechnum*; or, the margin of the frond is split and the sporangia are hidden in the narrow cleft thus made, as in *Vittaria* and *Schizoloma*. Often the margin of the frond is folded over, thus covering the sporangia, which are here developed on raised cushions; *Allosorus, Ceratopteris, Ceratodactylis, Parkeria,* and many other genera exhibit this formation. The extreme variety prevailing in this class of adaptation is connected with differences in the climatic conditions of the habitats where the plants in question live. Any attempt to deal with individual contrivances here would lead us too far.

The Rhizocarpeæ are a group nearly allied to Ferns, and they naturally follow the same lines as Ferns in the formation of their spores and sporangia. *Salvinia* reminds one to some extent of the Hymenophyllaceæ, at any rate as regards the outgrowth of an annular wall below the sporangia (the latter being in this case also borne on a fusiform axis), and also as regards the development of this wall, which becomes closed at the top into a complete box enshrouding the sporangia. *Marsilea*, on the other hand, exhibits stalked, bean-shaped capsules with cavities in which the sporangia are formed on raised cushions.

The Club-mosses (Lycopodiaceæ) also bear a striking resemblance in their mode of spore-formation to Ferns, especially to the various species of *Lygodium* and *Lygodictyon*, genera of which mention has already been made. The first rudiments of the sporangia are swellings at the base of the little squamiform leaves, or on the axis just at their insertion. The internal tissue of this protuberance is marked off in the form of a roundish ball. The cells constituting the ball separate and then become segmented each into four chambers, the walls of which are subsequently dissolved. The protoplasts within the chambers inclose themselves in membranes and become free spores. The epidermis originally clothing the swelling persists, and now forms the wall of a bean-shaped sporangium containing loose spores. The sporangium subsequently opens by means of a lid like a box.

Horse-tails exhibit a process of spore-formation quite peculiar to themselves. Two species of this group—namely, *Equisetum arvense* and *E. sylvaticum* are shown in figs. 190^2 and 190^7. At the top of the hollow stem there is a spike of peltate scales borne on short stalks and arranged in whorls, each of which must, in consideration of its origin, be looked upon as a metamorphosed leaf (*cf.* fig. 190^3).

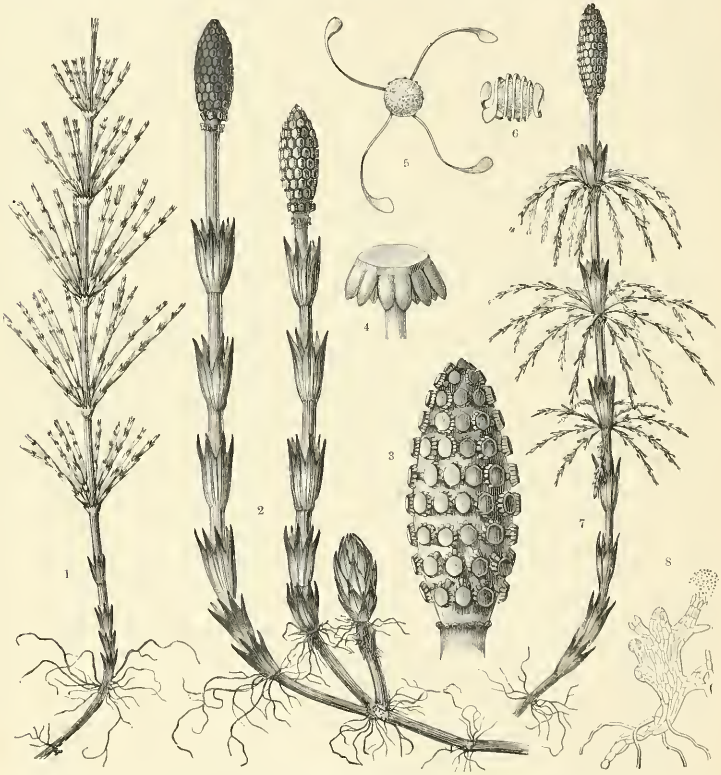

Fig. 190.—Horse-tails.

^{1} Summer Shoot of *Equisetum arvense.* ^{2} Vernal fertile Shoot of *Equisetum arvense.* ^{3} Spike of whorled sporangiophores from the same *Equisetum.* ^{4} A single sporangiophore. ^{5}, ^{6} Spores. ^{7} *Equisetum sylvaticum.* ^{8} Prothallium of a Horse-tail. ^{1}, ^{2}, ^{7} natural size; ^{3} × 3; ^{4} × 6; ^{5}, ^{6} × 25; ^{8} × 30.

On the inner surfaces of the scales—*i.e.* those turned towards the axis of the spike—little warts arise, which develop into sporangia (*cf.* fig. 190^4). The outer cell-layers of these multicellular warts become the walls of the sporangia, whilst the inner tissue breaks up into cells. These cells then divide into four cells, each of which becomes a spore.

The last division of plants wherein the spores are formed deep down in a tissue is that of the Muscineæ, which include Mosses and Liverworts. In these plants the spore-producing generation consists of a cellular body, which has arisen from the fruit, is usually seated on a stalk, and in shape is cylindrical, pyriform, or more or less spherical (*cf.* figs. 191 $^{3, 4, 7, 8, 15}$). We must here remark, by the way, that botanists used formerly to look upon this sporogenous generation of the Moss erroneously as the fruit itself. The only structure rightly to be considered as the Moss-fruit is that in which the embryo is produced as a result of fertilization. If afterwards a new generation springs up from the embryo which has been formed in the interior of the fruit, this generation cannot any longer be described as a fruit even in cases

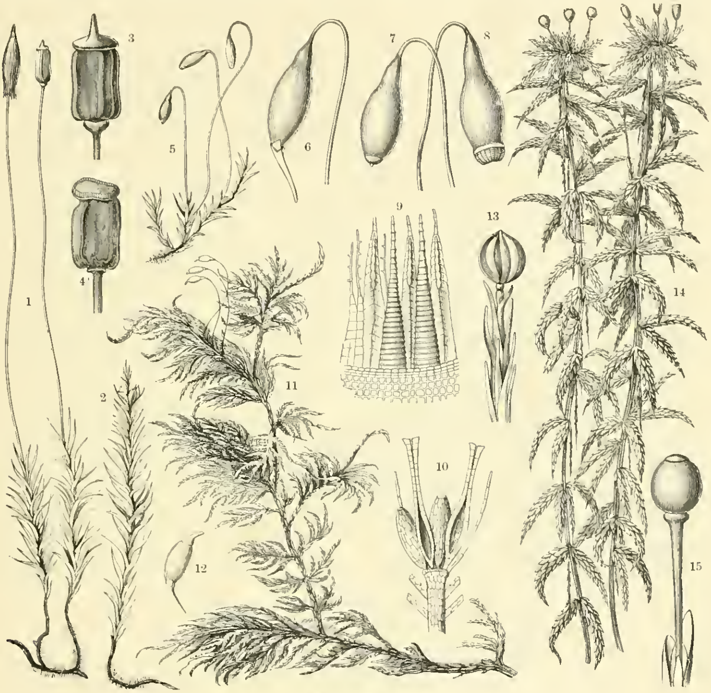

Fig. 191.—Mosses.

^{1} *Polytrichum commune*, the sporogonium to the left concealed by the cap, the sporogonium to the right exposed. ^{2} The same Moss in an earlier stage of development. ^{3} Sporogonium of *Polytrichum commune* with its lid. ^{4} The same after the lid has fallen off. ^{5} *Bryum cæspiticium.* ^{6} Sporogonium of the same Moss with its cap. ^{7} The same without the cap, but with the lid still on. ^{8} The same after removal of the lid, showing the teeth (peristome). ^{9} A piece of the peristome. ^{10} Antheridia, Archegonia, and Paraphyses of *Bryum cæspiticium.* ^{11} *Hylocomium splendens.* ^{12} Sporogonium of *Hylocomium splendens.* ^{13} *Andræa rupestris* with burst sporogonium. ^{14} *Sphagnum cymbifolium*, its spherical sporogonia still covered by their lids in the left-hand specimen. ^{15} A single sporogonium of the same Moss. ^{1}, ^{2}, ^{5}, ^{11}, ^{14} natural size; ^{3}, ^{4}, ^{6}, ^{7}, ^{8}, ^{12}, ^{13}, ^{15} × 5; ^{9}, ^{10} × 150.

where it remains permanently connected with the mother-plant, as happens in Mosses.

The cells composing the tissues of the cylindrical, pyriform, or spherical body above referred to develop in a variety of ways. Those situated near the outer surface form the wall of a receptacle, and those in the interior, which serve as a filling to the receptacle, form the spores. The process of spore-formation is here much the same as in Ferns. The cells of the central mass, at first united into a tissue, in time become isolated; each divides into four, and the spores are ultimately developed from these protoplasts. The spores are then left free in the form of a fine powder within the receptacle, which is called a sporogonium. In most Liverworts, a group nearly allied to the Mosses, certain other cells having a curious structure are formed from the internal tissue besides the spores. These are the so-called "elaters", and they serve to scatter the spores. In a few Mosses a sort of central column remains in the middle of the sporogonium in addition to the spores when the whole is mature. Externally the sporogonia of Mosses differ very little from the cellular bodies out of which they were developed; like them, they are spherical, pear-shaped, or cylindrical as the case may be. But the part which subsequently opens and liberates the spores at the proper time exhibits in its more minute anatomy considerable differentiation. This subject and that of the elaters mentioned above will be again referred to in the section devoted to the distribution of spores.

As with the sporangia in Ferns, so also in Mosses the sporogonia are protected during development from injurious external influences, especially desiccation, and are wrapped in coverings which vary considerably according to their origin. In Mosses a kind of cap is usually to be seen covering the young and tender sporogonium (see fig. 191 [1]), and this structure has its origin in the fruit from which the sporogenous generation (or *sporophyte*) has sprung, the coat of the fruit being torn away and its upper part carried up in the form of a cap by the sporophyte during its growth from the embryo. Later on, when the sporogonium is no longer in need of protection, and the presence of a cover would be detrimental in that it might prevent the spores from being scattered, the cap is cast off.

All the spores hitherto discussed originate within a tissue, and their history involves the conversion of the protoplasmic contents of each compartment of the reproductive part of the tissue into a spore. A second group of spores is composed of those which arise from the breaking up of the protoplasmic contents of tubular, club-shaped, or spherical cells not united in tissues, and are set free from their birthplaces as soon as they are formed. The cells thus constituting the mother-cells of spores may, by analogy, be conveniently termed sporangia. The process of formation of spores within them appears to be much simpler than in Ferns, Club-mosses, Horse-tails, Mosses, and Liverworts. Speaking generally, the only striking differences occurring in these cases are such as affect the number and shape of the spores which escape from a sporangium.

As described in the first volume of this work (*cf.* vol. i. p. 23, and Plate I. *a*–*d*), the filamentous organism *Vaucheria* produces a single comparatively large green spore in each of the club-shaped outgrowths developed by the tubular branches of the plant, and each spore thus formed is able, when free, to swim about by means of its numerous short cilia. On the other hand, the mould-like Saprolegniaceæ, which live under water upon decaying animals, develop a large number of colourless spores in their clavate filaments, and these after escaping from the tubes whirl about in the water by means of two long revolving cilia (*cf.* fig. 192). In both these instances the spores themselves possess the power of movement and of swarming about in water, whence they are called "swarm-spores". The name "zoo-spores" (ζῷον = animal) has also been applied to them on account of their decided resemblance in form and behaviour to certain Infusoria.

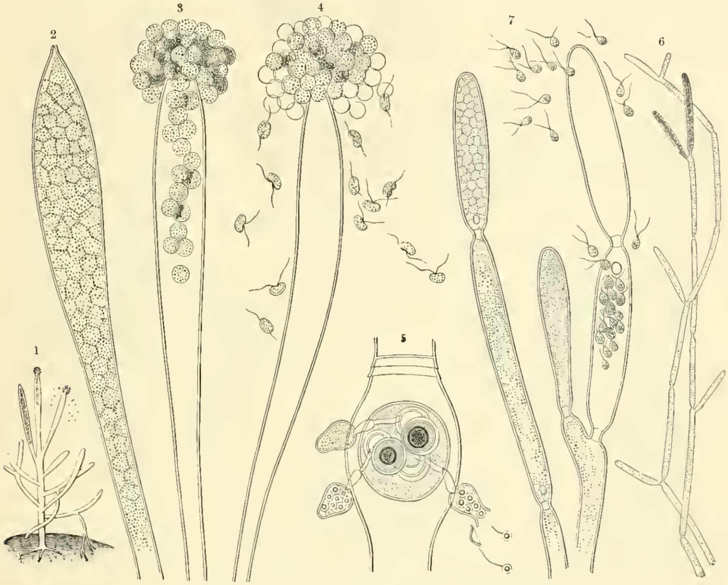

Fig. 192.—Swarm-spores of Saprolegniaceæ and Chytridiaceæ.

¹ *Achlya prolifera.* ², ³, ⁴ Development and escape of swarm-spores of *Achlya prolifera.* ⁵ *Chytridium Ola* parasitic upon the oogonium of *Œdogonium*; development and escape of swarm-spores. ⁶ *Saprolegnia lactea.* ⁷ Development and escape of the swarm-spores of *Saprolegnia lactea* (partly after De Bary and Pringsheim). ¹×20; ², ³, ⁴×400; ⁵×300; ⁶×100; ⁷×300.

The delicate, profusely-branched mycelia of the Moulds, included under the name Mucorini, give rise to special filaments which grow straight upwards. These erect hyphæ divide into two cells. The upper cell becomes a spherical bladder, and the under a long slender stalk, the upper end of which protrudes in the form of a hollow stopper into the bladder supported by it (*cf.* fig. 193 ²). The protoplasm in the upper vesicular cell breaks up into a large number of spores and thus becomes a sporangium. The increase in weight of the sporangium causes the filiform stalk to bend; the sporangium bursts, and the spores, together with the clear fluid in which they are suspended, issue through the rent in the sporangium (*cf.* fig. 193 [1]).

In the Moulds of the family of the Mucorini the sporangia are for the most part closely crowded together, but they are never walled in by a tissue or surrounded by any particular envelope. They are, moreover, always separate, and have the appearance of a miniature plantation. A different state of affairs is found in that group of Fungi known as the Ascomycetes, a group which includes, amongst well-

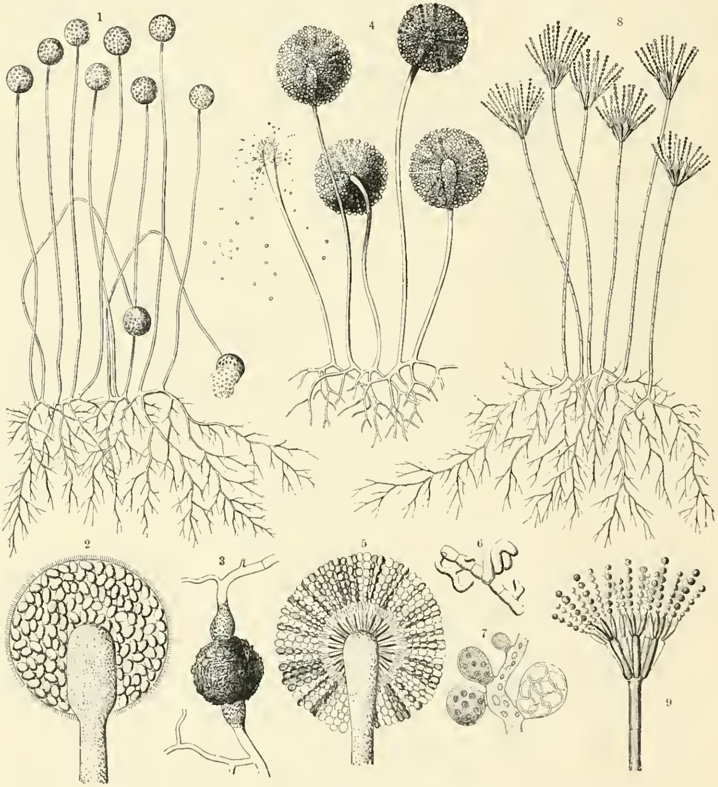

Fig. 193.—Moulds.

[1] *Mucor Mucedo*; ×40. [2] Longitudinal section of a sporangium of *Mucor Mucedo*; ×260. [3] Fruit-formation in *Mucor Mucedo*; ×180. [4] *Aspergillus niger*; ×30. [6] Longitudinal section of a sporophore of *Aspergillus niger*. [6] Fructification of *Penicillium crustaceum* (after Brefeld). [7] Fruit-formation in *Aspergillus* (after Eidam). [8] *Penicillium crustaceum*; × 40. [9] Sporophore of *Penicillium crustaceum*; ×200.

known plants, the genera *Morchella* and *Helvella* (*cf.* fig. 194), Lichens, and also several mould-like forms, notably the Erysipheæ, which produce Mildew, and *Claviceps*, which is the cause of Ergot of Rye. In these plants the ends of the hyphæ stand up from restricted areas of the mycelium, some in the form of long clavate tubes, some as delicate filiform paraphyses, the group of tubes and paraphyses being surrounded by other cellular structures in such a manner that the whole has the appearance of a dish or cup or capsule. The protoplasm in the tubes breaks up and forms either ellipsoidal bodies arranged usually in linear series (*cf.* fig. 194 ^{2}) or long fascicled threads, which, whilst still inclosed in the tubes, put on a stout cell-wall. The name of *asci* (ἀσκός = a leather bag) has been given to these sporangia, and *ascospores* to the spores which they contain. They are destitute of cilia, the distinguishing mark of zoospores, and have no power of independent motion after their extrusion from the tubes, which takes place through a rent at the top.

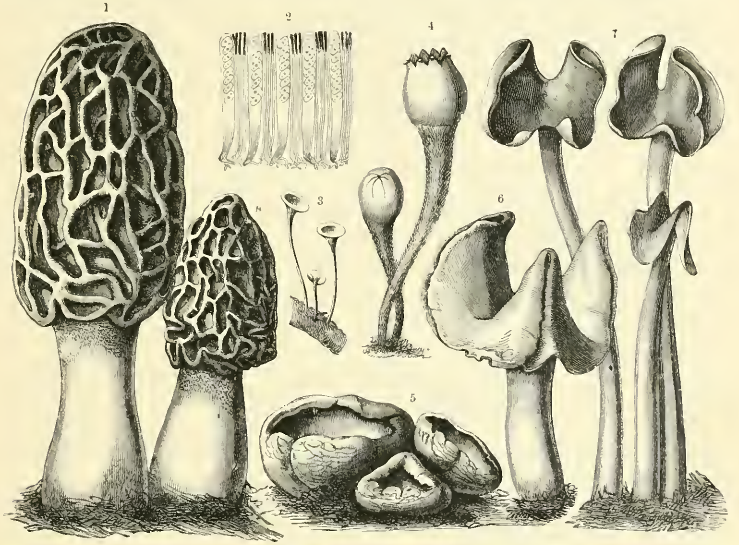

Fig. 194.—Discomycetes.

[1] The Morel (*Morchella esculenta*). [2] Longitudinal section from the hymenium of *Morchella esculenta* showing five filaments each containing eight spores and filiform paraphyses in between them. [3] *Helotium Tuba.* [4] *Anthopeziza Winteri.* [5] *Peziza vesiculosa.* [6] *Helvella Infula.* [7] *Helvella fistulosa.* [1], [4], [5], [6], [7] natural size; [3] × 4; [2] × 120.

There is great variety in the mode of grouping, as also in the envelopment of the sporogenous tubes in different genera and species. When the tubes grow from the bottom of flask-shaped excavations or pits, the whole structure is spoken of as a *perithecium*; if they stand in a shallow patelliform cavity or on the surface the term used is *apothecium*. Perithecia and apothecia have been erroneously called fruits also. The same principles must here be applied as governed our consideration of Ferns and Mosses. Even if the genesis of perithecia and apothecia is really preceded by a process of fertilization, still the only part properly to be called a fruit is the tissue in which one or more protoplasts have become embryos in consequence of the act of fertilization. The outgrowth from this fruit is precisely the new generation; and it does not matter at all whether this new sporogenous generation preserves its connection with the previous fruit-forming generation or not. Perithecia and apothecia, and, in general, all so-called fruits in the Ascomycetes are therefore equivalent to the sporogonia in Muscineæ and to the sporangiferous plants in Horse-tails, Club-mosses, and Ferns.

We shall place together in a third group all spores which arise neither singly in the cell-compartments of a tissue nor through the breaking up of the protoplasm within a tube, but by abstriction and abjunction. The process of spore-formation in these cases is as follows:—The protoplasm, which is inclosed in a cell-wall, produces an internal partition whereby it is itself divided into two halves, and the cell-cavity into two chambers. As soon as this has taken place the partition-wall splits and the two cells fall asunder. If the cell which undergoes the process of bipartition is in the form of a blind tube or sac, and if the partition is intercalated near the tip of the sac, the effect produced is as though the end of the sac had been tied off or abstricted and had then dropped. The part remaining behind now constitutes another blind sac, and in some genera the process of abjunction from the extremity may be repeated over and over again. *Basidium* is the name given to a closed sac of this kind from which spores are abstricted, it forming in a manner a base for the spores. This term has hitherto only been employed by botanists in relation to the so-called Basidiomycetes (which includes the Fungi known as Mushrooms and Toadstools), but it is justifiable to extend its application to all other structures which play the same part.

Abstriction of spores is exhibited at its simplest in the plant known as the Rust of Wheat, which at a certain stage of its development lives as a parasite in the green tissue of the leaves of our species of Wheat. For the purpose of spore-formation tufts of hyphæ project beyond the surface of the infested leaves. At the extremity of each hypha, which is in the form of a closed sac, a single spore of comparatively large size is developed; and after the fall of this one spore the hypha or basidium has lost the power of abstricting others.

A similar phenomenon is observed in the Fungi belonging to the genera *Hydnum*, *Polyporus*, *Agaricus*, and *Clavaria*, of which several examples are represented in fig. 195. Their basidia are club-shaped, and terminate in four slender filaments, the so-called *sterigmata*, and from the end of each sterigma one spore is abjointed (fig. 195 ^{7}). These basidia, together with a number of slender sac-like tubes, to which reference will again be made when the Basidiomycetes are described in detail, beset certain structures projecting from the under surface of the cap-shaped sporophore — these structures being lamellæ or spikes or tubes as the case may be. *Aspergillus niger* (see fig. 193[4] and 193[5]), a Mould living chiefly on the juices of fresh or preserved fruits, develops slender upright hyphæ with swollen ends, which bear numbers of short peg-like processes—the sterigmata—from which moniliform series of from five to eight spores are abjointed in rapid succession. These spores at first hang loosely together, and are arranged like strings of pearls, but collectively these rows of spores form a spherical head. A shock of any kind, especially the disturbance occasioned by currents of air, will cause a severance of the spores, and the entire sphere consequently falls to pieces.

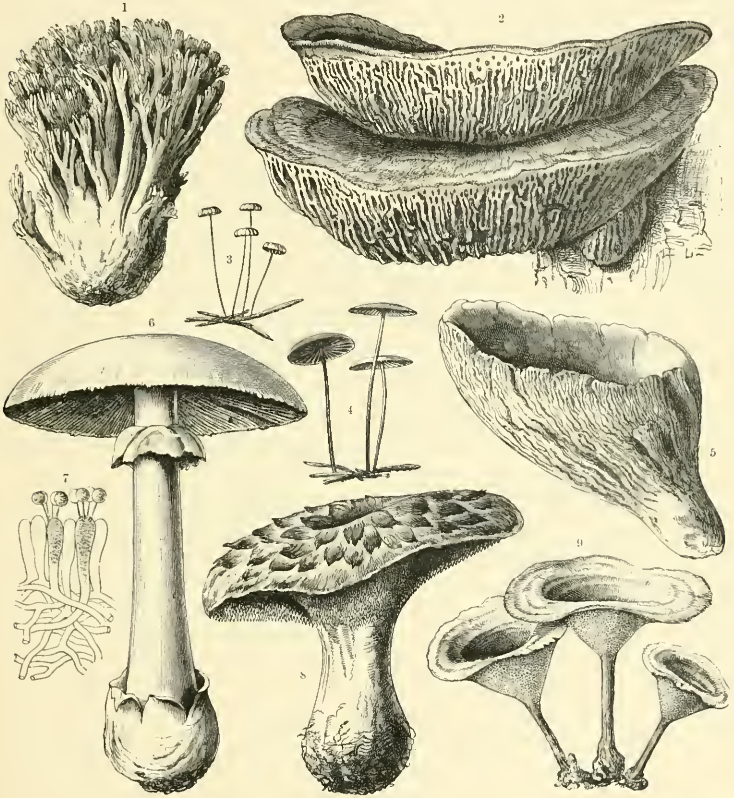

Fig. 195.—Basidiomycetes.

^{1} *Clavaria aurea.* ^{2} *Dædalea quercina.* ^{3} *Marasmius tenerrimus.* ^{4} *Marasmius perforans* ^{5} *Craterellus clavatus.* ^{6} *Amanita phalloides.* ^{7} Clavate basidia with filamentous sterigmata, from the ends of which spherical spores are abjointed (from the hymenium of *Amanita phalloides*). ^{8} *Hydnum imbricatum.* ^{9} *Polyporus perennis.* ^{1}, ^{2}, ^{3}, ^{4}, ^{5}, ^{6}, ^{8}, ^{9} natural size; ^{7} × 250.

Nothing then remains but the hyphal filament with its swollen end beset with pegs and looking like a club armed with spikes (*cf.* fig. 193 [4]).

Also in *Penicillium*, the commonest of all Moulds, the spores are abjointed from the sterigmata in moniliform rows; but in this case the erect hypha which bears the spores is septate and not clavate at the extremity, and terminates in forked branches, so that the chains of spores are grouped like the hairs in a camel's-hair pencil. A species of *Penicillium*—viz. *P. crustaceum*—is represented in fig. 193 [8] and 193[9]). In the Peronosporeæ, to which class belongs the parasite *Cystopus candidus*, celebrated for its fatal effects on cruciferous plants, moniliform rows of spores are abjointed from the basidia without the intervention of sterigmata. The mode of arrangement of the chains of spores in this parasite is, however, not quite like that in either *Penicillium* or *Aspergillus*.

A further diversity in this kind of spore-formation by process of abjunction is introduced by the presence in several families of plants of special envelopes surrounding the abjointed spores. Particular cases of this are afforded by Gasteromycetes (Puff-ball family) and Florideæ (Red Seaweeds) and by that stage in the development of the Rust-Fungus which is known by the name of *Æcidium*. The æcidia make their appearance in the form of structures growing out from a mycelium infesting the green tissues of leaves. The basidia are formed by the ends of hyphæ which stand up in dense crowds. Moniliform chains of spores are abjointed from the basidia and are enveloped by a sporangium-like wall developed from the cells surrounding the basidia. It is not till this enveloping capsule bursts that the spores are set free and can be distributed.

In the large Puff-Ball family (Gasteromycetes) the same process takes place, but the basidia and spores are not arranged so regularly, and amongst the spores are to be found other hair-like, cellular structures which constitute what is termed a *capillitium* and are of especial importance in relation to the distribution of the spores. Florideæ develop their spores within receptacles peculiar to themselves, which frequently resemble urns or capsules, and might be designated sporangia for the sake of terminological uniformity. The spore-filled "sporangia" of Florideæ, like those of Muscineæ—and in particular of Liverworts—are to be conceived as a separate generation, and, moreover, as a generation springing from cells which have undergone fertilization and have thereby been converted into fruit. The description of the process of fertilization must be postponed to a later section of this book; we have only to notice here that short cells are put forth as branches from the fertilized cells, and that some of these branches abjoint clusters of spores whilst the others develop into a sheath enveloping the assemblage of spores thus produced.

Under the name of Thallophytes are included all such plants as are destitute of vascular bundles and therefore are never developed into real *plant-bodies* (*cf.* vol. i. pp. 590–592). It often happens that Thallophytes form, in addition to the unicellular brood-bodies to which the name of spore must be limited, cell-aggregates which sever themselves from the thallus and become independent, the genesis of which has not been in any way a result of fertilization. These aggregates of cells are, in a manner, structures intermediate between the unicellular spores and the buds, differentiated into axis and leaves, which occur in vascular plants. They are portions of the thallus which produced them, and are either very like it or assume the same form as soon as their further development is complete. Hence the most appropriate name for these bodies is that of *thallidia* (θαλλός = young shoot; εἶδος = a likeness). They are also known as *gemmæ*. Thallidia are sometimes in the form of rows of cells, as, for example, those developed on the leaflets of the Moss *Syrrhopodon scaber* (see figs. 196$^{12, 13, 14}$); sometimes they are nets, as in the Water-Net (*Hydrodictyon*, see figs. 197$^{1, 4, 5}$). In the Moss *Tetraphis pellucida* (see figs. 196$^{4, 5, 6, 7, 8}$) they occur as plates of cells, and in other cases they assume the form of globular or ellipsoidal lumps of tissue, as, for instance, in the Moss *Aulacomnion androgynum* (see fig. 196$^{15, 16, 17, 18}$). Sometimes the number of cells associated

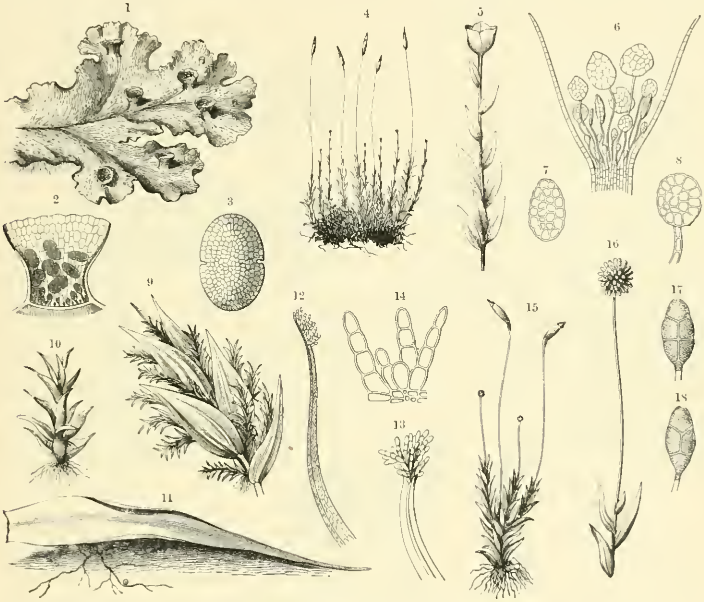

Fig. 196.—Thallidia of Muscineæ.

^{1} *Marchantia polymorpha* with cups containing thallidia or gemmæ. ^{2} Longitudinal section of thallidial or gemmiferous cup. ^{3} A single thallidium. ^{4} *Tetraphis pellucida.* ^{5} A stem of *Tetraphis* bearing a cup containing thallidia. ^{6} Longitudinal section of a thallidial cup. $^{7, 8}$ Isolated thallidia of *Tetraphis.* ^{9} A stem of *Leucodon sciuroides* with brood-bodies. ^{10} A brood-body set free from the stem. ^{11} Development of a brood-body from the rhizoids of a leaflet torn from *Campylopus fragilis.* $^{12, 13, 14}$ Development of thallidia at the apex of a leaf of *Syrrhopodon scaber.* ^{15} *Aulacomnion androgynum.* ^{16} A stem of the same bearing thallidia. $^{17, 18}$ Single isolated thallidia. ^{1} natural size; $^{4, 15}$ × 2; $^{2, 12, 13}$ × from 8 to 15; $^{5, 6, 9, 10, 14}$ × from 20 to 40; $^{3, 7, 8, 17, 18}$ × 120.

in a brood-body of the kind is limited to two, as is the case in the so-called "teleutospores" of the Rust-Fungus; whilst those of Florideæ sometimes have four cells and are known as "tetraspores". Again, in other cases hundreds of cells are associated together to form a thallidium, an instance of which is afforded by the brood-body or gemma of *Marchantia* (see fig. 196^{1,2,3}). The "soredia" of Lichens must also be brought under this head—by the term soredia being understood certain bodies which arise upon the thalli of Lichens and consist of one or more green cells wrapped in a net-work of colourless hyphæ (see vol. i. p. 248).

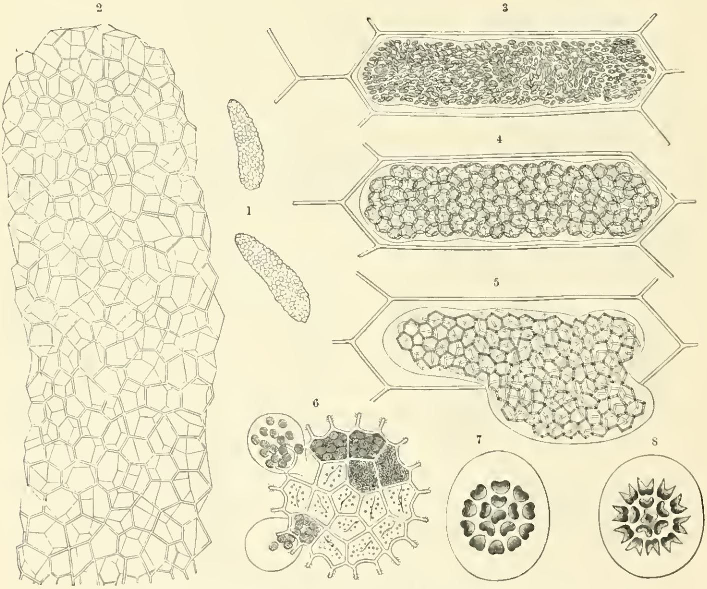

Fig. 197.—Formation of Thallidia in the cells of *Hydrodictyon* and in those of *Pediastrum*.

^{1} Water-Net (*Hydrodictyon utriculosum*), natural size. ^{2} A piece of the Water-Net; × 50. ^{3}, ^{4}, ^{5} Development and escape of a reticulate thallidium; × 300. ^{6} *Pediastrum granulatum*; development and escape of thallidia; the lightly-dotted cell chambers already vacated. ^{7}, ^{8} Thallidia of *Pediastrum* after their escape; × 240.

Thallidia may originate in the interior of a cell-cavity of the parent-plant and escape in the form of complete, though extremely minute, cell-aggregates Instances of this are afforded by the Water-Net (*Hydrodictyon utriculosum*) which is shown in fig. 197^{5}, and by *Pediastrum granulatum* (fig. 197^{6}), an organism of frequent occurrence in pools. The alternative method of formation of thallidia is by the severance of groups of superficial cells, which, after an interval of peregrination of variable duration, fasten on to some spot or other and found a new colony. In many Liverworts and Mosses special pockets and cups are produced, within which thallidia are continuously developed in the manner shown in figs. 196 [1, 2, 3, 4, 5, 6, 7, 8].

The formation of these brood-bodies by Lichens and Mosses may be induced by wounds or mutilations affecting the plants in question; but the stimulus is not here susceptible of being so clearly and surely inferred from its effects—and perhaps has hardly yet been so carefully investigated—as in the case of trees, shrubs, and herbs, which, being planted on a large scale, have afforded experience for centuries with the result that the practice of inducing the formation of buds by mutilation and of using them for the purpose of artificial propagation is extremely common in cultivation. Parasitic thallophytes receive an evident stimulus to the formation of brood-bodies upon the death of their hosts. As long as the host-plant is healthy and vigorous the parasites keep their hyphæ and suckers buried within the nutrient tissue. They there consume all there is to consume, increase in size, and thread their way through wood and green tissue in ever-widening circles—but without ever forming brood-bodies. Not until the host is quite exhausted and languishing at death's-door does the parasite, to avoid the danger of perishing with its foster-parent, provide for its departure from the ruin, and it is then in the form of brood-bodies that it escapes from the tissue it has ravaged. Here and there some of the tubular cells grow quickly from the interior of the dying tissue of the host-plant and emerge to the surface through stomata or rotten cell-walls. All the substance contained in the cells of the parasite becomes concentrated at these new foci of formative activity, and here masses of spores and thallidia are developed and abstricted at the very points where most extensive distribution is rendered possible by currents of air and water. Thus, the parasite is resolved into a number of brood-bodies and abandons the mansion which it has brought to destruction.

BUDS ON ROOTS.

Just in front of the house in which I am writing there used to stand years ago a great Aspen. The tree was felled, the axe being laid so close to the earth that only a stump projecting a few centimetres above ground was left. In the following spring the stump became the centre of quite a grove of Aspens, slender shoots having pushed through the grass over a large circular area round the stump. At first the shoots appeared one by one, then by dozens, and at last by hundreds at a time. They grew up into trees, and now, instead of the single Aspen, there is a little wood composed of trees which have not sprung from seed, but from the subterranean roots of the felled Aspen. Before the old tree had been deprived of its trunk and foliage its underground roots produced lateral roots only, which grew in a plane beneath and parallel to the surface, and continued to spread so long as they did not encounter any insuperable obstacle. Suddenly there was a change in the processes going on in this root; its formative energy was no longer devoted to the development of lateral roots, but was directed to the construction of buds from which green leafy shoots sprang up above the surface of the ground.

A forester of the old school, whose attention I drew to the above phenomenon with a view to ascertaining how he would explain it, told me that when the tree was cut down the flow of sap destined for the nourishment of the trunk and its crown of foliage was arrested in the roots underground, and thereupon sought an outlet elsewhere. Lateral roots having become useless, the diverted juices did not form them, but instead sent a great number of delicate shoots above the ground, because this was the only manner of preserving the life of the Aspen. At first sight this may seem to some people a foolish answer, and I have even heard it called absurd. Nevertheless we are obliged, after impartial consideration, to admit that we are not in a position to give any explanation which is not essentially the same. If we conceive the living protoplasts in the formative tissue of the roots as being the "juices" referred to by the forester, there is no longer any difference between his explanation and that given by Science. At the very spots where formerly lateral roots would have been developed, leafy stems are produced. The same protoplasts which now work at the construction of a bud would, if the tree had not been cut down, have fashioned a lateral root. That this alteration in active function was caused by the felling of the tree is certain, although no mechanical explanation of this stimulus can be given. The only possible source of excitation seems to be the checking of the egress of formative material stored in the roots in the direction in which it was formerly accustomed to flow.

Another special point of interest connected with the history of this Aspen is that for the most part the roots, after giving rise to a series of shoots, died and decayed, whilst the shoots developed into separate and independent trees, each furnished with roots of its own, so that they look as if they had been deliberately planted in the earth in rows. As a matter of fact, however, the Aspen itself produced these saplings from its subterranean portions, and planted them out, thus not only renewing its own youth but multiplying. For such multiplication it is evidently necessary that some cell in that part of the root which possesses the power of growth should form the starting-point or rudiment of a new shoot. The cell chosen for the purpose divides into daughter-cells, and these again become subdivided; but several adjacent cells also participate in the new fabrication, and we can picture to ourselves the process as the action of a group of protoplasts located within the limits of the living and formative tissue of the root, which separate themselves off from the rest and form a confederation of mutually helpful associates with the common function of constructing the new shoot. Neither the protoplast in the mother-cell of the young shoot nor the adjacent protoplasts undergo any stimulation by neighbouring cells before beginning their work. No process of pairing takes place. The phenomenon of renewal and multiplication of the Aspen which goes on before our eyes must therefore be classed as a case of asexual reproduction. The fact that a single root of the Aspen, instead of producing one sapling only, gave rise to ten, obliges us to suppose that these protoplasts of the growing tissue of the root, which separated themselves off under the influence of the new conditions created by the felling of the tree, arranged themselves in ten groups and each group from that time forth devoted itself to the new task of furthering the growth of the shoot developing at its centre. On investigation we find that these aggregations of cells are invariably situated in the deeper layers of the rind. In the first place a delicate tissue is developed from a particular cell which dominates the entire group and governs the process of construction. This tissue pushes outwards, on the one hand, towards the superficial layers of the rind, whilst, on the other hand, it sends a shaft inwards into the cambium layer of the root. Immediately afterwards vascular bundles are developed, and the shaft-like rudiment of the young bud is through them placed in connection with the woody tissue of the root, and when all this is finished the rind is finally broken through, and a bud clothed with leaves behind its growing point bursts out through the opening.

These buds, and the shoots arising from them, are termed radical buds and shoots. They are anything but rare, and it would be an error to suppose that they only occur on the Aspen because that tree has been chosen to illustrate the subject. Not only a great number of trees, but also many shrubs, and a host of herbaceous plants, great and small, exhibit this kind of revival and multiplication, and for many species it is the safest and most fruitful mode of reproduction. It would also be wrong to suppose that radical buds only arise when the aërial parts of the plant concerned have been injured or destroyed in consequence of some unusual occurrence. A shock of the kind is certainly the most frequent cause; but it is equally certain that of trees and shrubs not a few develop rudimentary buds on their roots when their time comes—*i.e.* when they have become decrepit, and one branch after another is dying—without their having suffered any injury from worm or weather, or from the woodman's axe. A profuse after-growth of young plants always springs from the roots and surrounds old and dry trees of the following kinds:—the Aspen (*Populus tremula*), the Tree of Heaven (*Ailanthus glandulosa*), the Tulip-tree (*Liriodendron tulipifera*), and the Osage Orange (*Maclura aurantiaca*), and the same statement applies to the following shrubs when they begin to wither—the Raspberry (*Rubus Idæus*), the Sea-Buckthorn (*Hippophae*), the Hawthorn (*Cratægus*), the Barberry (*Berberis*), the Lilac (*Syringa*), and the Rose (*Rosa*), and to many other woody plants; whereas, no such "breaking" from the root is seen on young specimens of the above unless there has been some previous injury to the parts above ground.

The budding power of roots is made use of by gardeners for the purpose of artificial propagation. They cut pieces from the roots of the plants they wish to multiply and insert them in soil which is kept moist, and they may then count almost with certainty upon the development of several buds on each separate piece of root. This mode of propagation by root-cuttings or slips, as they are called, is attended by particularly successful results when applied to the flowering trees or shrubs of *Cydonia Japonica*, *Paulownia imperialis*, *Tecoma radicans*, *Dais cotoni-*

folia, and to various species of *Acacia, Halesia, Hermannia*, and *Plumbago*. Moreover, the development of buds on roots is observed to take place not only in trees and shrubs, but also in herbaceous plants; and, indeed, in some it is of regular, annual recurrence. As instances of this may be mentioned the Dwarf Elder (*Sambucus Ebulus*), *Asclepias Cornuti, Sophora alopecuroides, Lepidium latifolium*, the Dock (*Rumex Acetosella*), various species of the Toad-flax and Spurge (*e.g. Linaria pallida, L. genistæfolia, L. vulgaris, Euphorbia Cyparissias*), and several Composites and Pelargoniums. In another series of herbaceous plants the phenomenon occurs exceptionally as a result of special external conditions, and chiefly in consequence of injuries, as, for example, in case of damage to the roots of certain Orchids (*Epipactis microphylla, Neottia Nidus-avis*), or of the Adder's Tongue amongst Ferns (*Ophioglossum vulgare*). Nor must we omit to mention the buds which are formed on aërial roots. There is so regular a production of buds from the columnar aërial roots of tropical Fig-trees, and of leafy shoots from the buds thus developed, that at first sight one is inclined to take the root-columns for trunks.

BUDS ON STEMS.

Buds and shoots growing directly from a part of the stem are termed cauline buds and shoots. Any part of a stem may become the point of inception of a bud. The commonest positions occupied by buds are the regions of the stem which bear respectively scale-leaves and foliage-leaves, and this is especially the case with those buds which subsequently become brood-bodies. But also lower down and higher up buds are observed to develop, and do so, indeed, without the occurrence of any apparent injury or other assignable external cause. Thus, for instance, it frequently happens that buds are developed on the hypocotyl of the Scarlet Pimpernel (*Anagallis arvensis*), which abounds in our fields and kitchen-gardens, and the same is true of the species of Spurge (*Euphorbia Peplus* and *E. vulgaris*) which grow as weeds in company with the Pimpernel, and likewise of young Toad-flax plants (*Linaria vulgaris*), and of a few Umbellifers. These buds grow out immediately into green leafy shoots. In all probability the phenomenon occurs in many other plants besides, but hitherto the subject has received only cursory attention.

These buds on the hypocotyl are all the more worthy of notice because they emerge below the cotyledons and in no case from a leaf-axil, *i.e.* the angle formed by a leaf with the stem. In the region of the foliage-leaves it is comparatively rare for a bud to originate at any other spot than in the axil of a leaf. As instances may be mentioned the extra-axillary buds of the Nightshades (Solanaceae), the buds in *Serjania, Medeola asparagoides*, &c., which spring laterally from the stem close to the foliage-leaves, and those in the Vine and Virginian Creeper (Ampelideæ), which are set opposite to the foliage-leaves. But even in these cases the positions of the buds, relative to the foliage-leaves of the stem, are always such as to be most naturally explained by the need of the former to obtain the formative materials produced in the green tissue of the leaves, in order to complete their own development; and these materials are most directly conveyed to them if they are situated as near as possible to the spot where the vascular bundles of a green leaf lead into the stem.

When a large number of foliage-leaves are packed closely together upon a stem, it is scarcely possible for a bud to be developed in every axil. On such occasions the buds appear always to possess the power of selecting the most convenient points of origin. The majority of leaf-axils are altogether destitute of buds, and it is only at spots where their inception would be most favourable to the plant's development that a few hardy buds are put forth. This is what happens, for example, in most species of Spurge, in the Toad-flax, in Pines and Firs, in Araucarias, and the rest of the numerous family of Conifers. Where buds are formed in the axils of leaves, either there is one to each leaf, or several are crowded together in an axil, and of these one is conspicuous owing to its central position, and also usually for its size, whilst the rest are subordinate. The occurrence on the leafy region of the stem of buds crowded together in this fashion—the meaning of which will be examined in detail in the next few pages—is confined to certain species belonging to the Flora of the Mediterranean, of Australia, and of various Steppe-lands. They are much more commonly found on such regions of the stem as bear scale-leaves, especially in bulbous plants, which sometimes exhibit as many as a dozen little buds springing from the short, thick stem in the axil of one of the expanded scaly leaves of the bulb.

The buds produced in the floral region of the stem (or inflorescence) usually develop into flowers, and their function being the production of fruit, they cannot be considered until a later section of this work is reached. Meanwhile the bud-form of brood-body is not entirely absent from this region of the stem. Grasses, Saxifrages, and Polygonums afford a great number of examples of their occurrence in that position.

A wound may cause the formation of a bud at any altitude upon the stem. The bud invariably springs from the injured spot and often no relation can be detected between its point of insertion and the position of the leaves. An instance is known where the herbaceous stem of a Sea-Kale (*Crambe maritima*) was cut through transversely, and, after the pith had decayed, buds were formed on the inner surface of the vascular-bundle ring from the tissue of the so-called vascular-bundle sheath, and from the buds shoots eventually developed. If the main trunk or a branch of an Angiospermous tree, such as an Oak or Ash, is cut off smooth, a mass of tissue is formed from the cambium, thus exposed, at the boundary between wood and bast; this tissue gradually creeps out from the margins of the wound and swelling up takes on the form of a circular rampart. The wood-cells which have been cut through and left bare within the circumference of the rampart have not the power of dividing and multiplying so as to initiate a new structure, but are dried up by exposure to the air and perish. The tissue forming the rampart continues, however, to increase in breadth, and encroaches upon the dead interior of the section of the stump so completely that the cut surface of wood is quite covered over by the new growth. The latter is termed "callus", and may be compared to the tissue which is developed when an arm or a foot is amputated, and which grows from the ligaments beneath the skin until it gradually covers the whole stump. The callus in plants derives a special interest from the fact that within it are formed the rudiments of fresh buds, from which subsequently spring the shoots which "break" so plentifully. A longitudinal section through an Oak stump thus overgrown shows the callus wedged, as it were, between the old bast and the old wood; and we find that it consists of cork and parenchymatous cells, whilst vascular tissues, springing from the wedged portion of the callus, have also been developed, and, descending in bent and tortuous lines, establish an organic connection with the old trunk. The buds arising in the callus do not stand in any relation of any sort to the leaves, as has already been mentioned; nor do the intervals between them follow a geometric law, as is the case with the buds which take their rise from the axils of leaves. They are for the most part in aggregations and are produced anything but simultaneously. A callus of the kind may continue to produce buds at appropriate spots year after year, and shoots of many different ages may be seen springing from it. One cannot contemplate such a callus growth, covering a stump and sending out shoots as direct off-shoots of the decapitated trunk, without being involuntarily reminded of trees that have been "ennobled" by grafting in the manner described in vol. i. pp. 213, 214. There is also an analogy to certain parasitic plants, such as *Loranthus*, in which the connection with the host is established in exactly the same way as that between callus-buds and tree-stump by means of a tissue interposed between wood and bark (*cf.* vol. i. p. 211).

A formation of callus ensues upon the excision of the cortex from the side of a stem in the same manner as when the entire trunk is sawn through; and the process of covering up the exposed wood with callus, derived from the tissue lying between the bark and the wood, goes on similarly in the case of lateral injuries to the trunk. Some trees in addition exhibit a formation of callus without external damage having been received, as, for instance, the Ash, which has a bark liable to split and break open here and there spontaneously, whereupon a tissue of the nature of callus is formed in the open places. Oldish trunks of the North-American Ash (*Fraxinus nana*) are invariably covered with swellings and callosities of the kind, and most of them furnish starting-points for a score or more of buds.

The buds which spring from growths of callus on trunks must not be confounded with those called by foresters "dormant eyes" and "dormant buds". Nor must we fail to distinguish them from the structures which have been termed superposed and collateral buds, which whilst exhibiting extreme diversity in their various modes of development, yet all constitute contrivances for the preservation of the plants from destruction in that their function is to replace dead shoots. With reference to the part played by these structures, it is most convenient to classify them under the name of "reserve-buds". They either originate simultaneously with those which they are destined in certain circumstances to replace, or they are only subsequently formed in the cortex in the immediate neighbourhood of the points of origin of shoots which have already withered. The latter is of comparatively rare occurrence. In *Spartium scoparium*, which is represented in vol. i. p. 331, one bud only is produced in each axil. The following year, this bud grows out into a long switch, and at the same time a new bud is initiated in the cortical tissue just beneath the base of this shoot. If the first shoot dies next year, as often happens, especially in the case of plants growing near the northern limit of the Mediterranean region, the second bud produces a shoot, and close under its base is formed once more the rudiment of a bud for future substitution. This may go on for several years until at last a whole row of withered stumps are to be seen above the last substituted shoot. This mode of growth, which has been observed not only in *Spartium*, but also in several allied Papilionaceæ belonging to the Mediterranean Flora, is very prejudicial to the freshness and vigour of the plant's appearance. The presence of a number of withered remnants crowded together produces an impression of disease and starvation; else, as an alternative, one is tempted to suppose that the bushes have been cropped by cattle, or annually truncated by man, whereas they themselves accomplish all these changes without any damage of the kind being inflicted.

In *Robinia Pseudacacia*, the plant known by the name of Acacia, a single bud is formed at first in the axil of each foliage-leaf. But later on the stem close to the thickened base of the petiole becomes hollowed out, and in the cavity thus formed little knobs arise underneath the first bud. Sometimes there is one only, sometimes there are two or even three. These knobs are nothing more or less than first rudiments of reserve-buds which develop in this position where they are sheltered and protected by the remaining portion of the petiole. If, as is often the case, in the following year the shoot put forth by the first bud dies, it falls to the uppermost reserve-bud to develop into a substitution-shoot, which may perish in its turn and be replaced by the next reserve-bud. The different species of the genus *Gleditschia* behave in precisely the same way as *Robinia Pseudacacia*, but in them the reserve-buds are only partially hidden beneath the remnant of petiole, and the power of forming new buds at the ends of the branches is here almost unlimited. In some species of *Gleditschia*, e.g. *G. Caspica*, a substitution of shoots, one for another, as they successively dry up, takes place for a period of ten or more years. The consequence is that the long branches of these trees are nodulated at the seats of origin of the buds, and the dried stumps of upwards of twenty short branches dating from previous years are seen crowded close together on these nodes.

In *Pterocarya Caucasica*, a Caucasian tree allied to the Walnut, a single bud is formed every year in the axil of each foliage-leaf, and this bud has the peculiarity of being elevated from 1·5 cm. to 2 cm. above the leaf-insertion. Whilst it is growing next year into a shoot, the rudiment of a reserve-bud is formed just above the original leaf-insertion, but it only develops in some subsequent year in the event of injury to the first shoot.

Far more common than the above are the cases where the buds which sprout in the first year and those which remain dormant until called upon to replace the earlier ones originate all together simultaneously. In the Common Elder (*Sambucus nigra*) two buds are formed one above the other in each leaf-axil; in the blue-berried Honeysuckle (*Lonicera cœrulea*) and in several of its allied species, three buds of almost equal size are superimposed one above another in a straight line in each axil. In the year following their formation, usually only one of them grows out into a shoot; the others stop as they are, and maintain their vitality for a couple of years in reserve and only then develop if the first shoot has met with destruction. The North-American False Indigo, species of which (*e.g. Amorpha fruticosa, A. glauca,* and *A. nana*) are cultivated as ornamental shrubs in European gardens, produces two buds of different sizes above each foliage-leaf, the larger of the two being placed just above the smaller. The former sends forth a shoot in the following year, the latter remains in reserve. If the shoot first developed withers, as very often happens, the reserve-bud sprouts, and the withered stump of the first shoot is then visible just above the fresh one. The North-American tree *Gymnocladus Canadensis* also exhibits on the upper ramifications of its powerful branches two superimposed buds above the insertion of each leaf; the larger is situated above the smaller, and the latter only develops into a shoot in the event of its being required as a substitute. Several other woody plants which, though their stems become very thick, possess neither the growth of a tree nor a symmetrical crown of foliage—such as the Judas-tree (*Cercis Siliquastrum*) and the *Forsythia viridissima* of Japan—put forth long switch-like shoots, the upper halves of which often die off during the winter. The buds on the lower surviving half of each shoot are very close together, and generally they are in pairs, the upper one in each pair being close upon the lower. Only the upper one of a pair is at first developed in the next year; the lower bud does not develop unless the other fails.

It is sometimes the case that the axil of every leaf produces three buds set side by side instead of one above another. The middle bud sends out a shoot in the following year whilst the lateral ones are left as a reserve. The year after, if the shoot has died, what happens is either that one of the two accessory buds develops—as, for example, in *Lonicera fragrantissima* and in the case of the long shoots of the Nettle-trees (*Celtis Tournefortii, C. orientalis, C. occidentalis*), or both accessory buds develop simultaneously—as in the Southern Reed (*Arundo Donax*) and in several species of the genus *Bambusa.* The species belonging to the genus *Zanthoxylon* form in each leaf-axil the rudiments of from nine to eighteen buds, of which the middle one is the biggest and grows out during the following year into a short or long shoot. The other smaller buds are kept in reserve in the cortex at the base of the shoot.

In the Tree of Chastity (*Vitex Agnus-castus*) four buds are set in the axil of each foliage-leaf. The central bud is the largest and a smaller one is situated underneath it, whilst the other two—also smaller—are posted to the right and left respectively of the first. Next year a shoot is put forth from the large central bud whilst the other three remain dormant. By the second year this shoot has probably perished, and in that case the little reserve-buds sprout. Their development is not infrequently simultaneous, so that here and there upon the tree we have tufts, each consisting of four slender shoots—one withered and three green—which all radiate from one point. If the three later shoots dry off at the ends, the buds on their basal parts produce fresh shoots, and the bushes present a bristly and not very ornamental appearance like besoms, especially when they are destitute of foliage.

A curious development of reserve-buds may also be observed in *Atraphaxis*, a ragged shrub indigenous to the Steppes of Southern Russia. Four buds are formed simultaneously and in close proximity to one another in the axil of every foliage-leaf. Of these a very small one is immediately above the insertion of the leaf; it has a large one above, and two of medium size on either side of it. The large bud becomes a leafy shoot and the small one a blossom. The two lateral buds are kept in reserve unchanged during the second year, and in some circumstances during the third also. If the shoot dies, the development of the lateral reserve-buds is proceeded with; but as soon as they begin to sprout, the rudiments of fresh reserve-buds are formed in the cortex to the right and left of those that are thus developing. Here again, the ragged habit of growth of the shrub is connected with its peculiar mode of bud-formation. The following case is also very common. Of a crowd of axillary buds, placed either side by side or one upon another, one or more produce flowering shoots. When the fruits generated in the flowers have dropped—an event in this connection equivalent to the fall of the shoots which bear them—and the spots of detachment are scarred over, the reserve-buds come into play for the first time. In *Spiræa crenata* there is only one such reserve-bud; in the Dwarf Almond (*Amygdalus nana*) and the Mahaleb (*Prunus Mahaleb*) there are two or three. The diversity amongst plants in this respect is almost endless, but the compass of this work does not admit of the subject being treated in greater detail. Seeing, however, that the facts involved have not received due consideration on the part of botanists, I should like to draw attention to the peculiar phenomena of development in *Buddleia, Rhodotypus, Fontanesia, Philadelphus, Rubus, Berberis, Caragana, Alhagi, Lycium,* and *Ephedra,* and also to point out that amongst woody, shrubby and suffruticose Steppe-plants, which are especially liable to frost-bite and desiccation, many exhibit highly interesting characteristics in their development of reserve-buds.

In Willows we find a form of reserve-bud which differs from all the rest. It is obvious at a glance that every bud on an annual shoot of a Willow is entirely shrouded by a single scale shaped like a hood. This bud-scale originates in the outer layers of the cortical tissue, and is, so to speak, a raised piece of the cortex covering the rudimentary bud. The large bud wrapped in this scale possesses an axis which has arisen laterally from the axis of the branch which bears the bud, and the vessels and cells of the wood may be followed uninterruptedly from the branch to the base of the bud. But, close to the latter, we also notice some very small bud-rudiments with no bundles running into them from the branch. They take their rise in a special cellular tissue intercalated in the cortex, and on a branch in its first year are not externally visible, because they are covered by the large hood-shaped scale. The tissue of cells from which these small buds spring might be compared to a callus if it were not produced on wholly uninjured branches and long before the formation of cracks and fissures in the bark. In the second year, when the large central bud begins to produce a lateral branch, throwing off the hood-scale and elongating its axis, the small buds also become visible in the form of spherical or oval knobs at the base of the new side-branch springing from the large bud. They do not, however, get larger or smaller, but remain completely dormant and unaltered. There is even a possibility of their never developing further, but in the event of the branch at the base of which they were produced receiving an injury and dying, they are aroused from their lethargy and grow out into leafy ramifications. It is obviously their function to replace such of their predecessors as fall victims to unfavourable external conditions.

The Crack-Willows derive their name from the extraordinary fragility of their branches. The hard bast and wood at the base of their one-year-old and two-year-old branches exhibit a peculiar structure, the result of which is that a slight shock is sufficient to sever the tissue, so that the branch breaks across at its base and drops off. It seems to be an advantage for these Crack-Willows to get rid of certain leafless and useless twigs which bear nothing but the scars of shed catkins, and are merely an encumbrance. Thus much is certain, that several kinds of Crack-Willow cast off spontaneously a number of these branches, and that the buds above described as lying dormant in the cortex put forth leafy shoots as substitutes. Similar phenomena may be observed in Poplars. But in them the twigs break off at a little distance from the base, and the substitution of green, leafy branches for those covered with dead excrescences is effected by means of reserve-buds preformed in the axils of former bud-scales. There can be no question of mutilation in these cases any more than in the autumnal shedding of leaves which takes place spontaneously for the benefit of the plants concerned, and is not susceptible to the influence of external conditions except inasmuch as the latter may accelerate or retard it.

In all the cases hitherto described, the substitution-buds are developed in the cortical tissue. At first, there is no direct connection between them and the woody tissue of the stem; it is only when these buds are roused from their lethargy, and called upon to put forth shoots, to replace anterior or collateral shoots which have fallen, that communication with the wood, and to that extent also with the current of crude sap, is set up by means of special conductive strands.

There is, however, another form of accessory bud, which is connected from the very beginning with the wood of the stem appertaining to it, and maintains this during its whole life. In forestry the name of "dormant eye" already referred to is employed in particular for this form of bud. If a year-old branch is examined, it is found that the buds in the leaf-axils of its upper half are strikingly larger and more vigorous than those near the base; indeed, above the point of insertion of the lowest scale-leaves of the branch, it is not even possible in most cases to detect so much as a swelling that might be construed into the rudiment of a new bud. It is not till a longitudinal section is made through the lowest part of the branch that one perceives the existence of buds, here, too, in a very rudimentary condition and buried in the cortical tissue. The large buds to be seen at the close of the first year about the middle and at the extremity of the branch develop next year into fresh branches, the lower parts of which are again clothed with bud-scales, and the upper parts with foliage-leaves; but the small, inconspicuous or invisible buds at the base of the first year's shoot are left undeveloped and completely dormant. They are preserved practically unaltered in size or shape at the spots where they originated within the cortex, in some cases showing above the surface, in others concealed by the outer coats of the bark; and the only change which takes place is that the bundles leading from the wood of the branch to the dormant buds elongate yearly to the extent of the thickness of the new woody ring. These bundles exhibit the same disposition as those within the shoots which are visible on the surface, and so far, we might look upon them as latent lateral axes or side branches imbedded in the wood of the main branch and terminating in dormant buds. The analogy is confirmed by the fact that the lateral axes buried in the wood are capable of ramifying in the same manner as those which project beyond the periphery of the stem and send their branches out into the air. The rudiments of fresh buds may also be formed on the concealed branchlets within the wood of the continually thickening main axis; and in many trees densely-branched structures terminating in dormant buds are formed in the wood of the stem, and exercise a disturbing influence on the course of the surrounding tubes and fibres of the wood of the main stem, causing them to bend and twist about to a very great extent. In this manner knobs of various sizes are formed, composed of the branched latent shoots which terminate in dormant buds and of winding wood-fibres. These nodules are found interspersed amongst the elements of the wood, which pursue a normal course, and they are known as "bird's eyes". Sections of such bird's-eye timber were much in demand some decades ago for use as veneering in cabinet-making, owing to the curious traceries exhibited by them, which usually take the form of eyes surrounded by rings and of serpentine lines—the former corresponding to latent branches, the latter to sinuous wood-fibres.

As already mentioned, in many trees and shrubs it is particularly the buds pertaining to the axils of the lowest leaf-structures that are kept back in a dormant condition. A striking deviation from this habit is exhibited by the Tamarisks (*Tamarix*). The young branches, covered with innumerable little leaves and an assemblage of buds—usually three in number—are formed in the axil of each leaf. Want of space would of itself be sufficient to make it impossible that all these buds should produce shoots in the following year and develop simultaneously; about a thousand lateral branches would in that case be produced simultaneously from an axis little over a metre in length. As a matter of fact only comparatively few of the buds produce shoots, and these are so aptly distributed that no one of them restricts the freedom of another by pushing it aside or competing for its supply of air and light. Hundreds of rudimentary buds, not only at the base but scattered over the entire length of the branch, remain dormant in the Tamarisk branch, as it grows thicker and thicker, and thus is explained the fact that shoots springing from such branches have an almost inexhaustible store of lateral shoots, and are capable of producing every year afterwards hundreds of fresh shoots.

Those reserve-buds which are formed in the cortical tissue and have no connection with the wood of the stem which bears them, for the most part maintain their vitality only for a few years. The dormant buds at the extremities of latent branches may, on the other hand, preserve their capacity for development for many years, although they undergo no change either in shape or in size. No doubt many of them die in the course of a year or two without being replaced by others; whilst many others which perish have their places filled by new ones developed at the ends of embedded branches. But these are rare occurrences in comparison with the large number of cases where dormant buds retain their vitality for many years.

Suppose the case of a tree one hundred years old, which has been shattered by a violent storm. With its crown of foliage torn down and its great branches broken off and strewn upon the ground, it reminds one of the ruins of a building of which roof, gables, battlements, and walls have been partially demolished. Where previously thousands of leafy boughs formed a spreading crown, now a few riven stumps are seen standing in dreary solitude. The tree has the appearance of being hopelessly destroyed, and one would anticipate that its trunk would dry up completely in the following year. Yet, marvellous to relate, fresh life quickens in the old and shattered trunk. Buds which have lain dormant in the cortex during scores of years stretch out, push their way through the fissures in the bark and develop into vigorous branches, and within a twelvemonth the thick stumps of the old trunk and branches are covered over with a drapery of fresh shoots which have buds set in the axils of their leaves. After another year has passed lateral branches develop from some of these buds, and this process continues until, in about ten years, the maimed tree becomes furnished with a new, densely-ramifying crown of foliage. Who, after witnessing such a phenomenon as this, can doubt that the arrested development of a portion of the cauline buds is an adaptation to ensure trees and shrubs against destruction in case of their being fractured by the wind or otherwise mutilated, or that dormant buds are to be looked upon as a reserve to meet possible accidents in the future!

The fact that twigs which have shed themselves or succumbed to adverse external influences are replaced out of the store of dormant buds or by the buds of the callus, has led to various interferences on the part of man with the natural growth of cultivated plants, and has given rise to a whole series of methods of propagation, which have been employed by farmers and foresters ever since ancient times. To this class of operations belongs, for example, the method employed to promote the growth of underwood, which mainly depends on the development upon the stumps left when the wood is cut, of new shoots from the callus or from the dormant eyes, shoots which in the course of thirty or forty years replace the old plantation, that is to say, the mass of wood which has been taken away. Pollarding is another instance. Pollard-trees are kept cut down to a particular height, and in consequence become thickened at the top, as may be seen in the case of Poplars, Ashes, and more particularly Willows. The pruning of Vines and Fruit-trees is likewise of this category, and the same process is applied also to the woody plants trained to form espaliers or hedges when a park is being laid down or an estate inclosed. All these manipulations have in view, on the one hand, a development of more vigorous shoots from the stumps that are left behind and the acquisition of as abundant a yield of timber, forage, or fruit as possible; on the other hand, a denser growth of the tree-top, or a stunting of the tree, such as is required for gardens in the old French style, with their formal green walls, obelisks, and marvellous ornamentation. Seeing, however, that each of the various trees and shrubs has peculiarities of its own in relation to the formation of callus and dormant eyes, many different modes of pruning are applied to them. We cannot generalize from one case to all the rest, and it would be a great mistake, for example, to try to pollard Apple-trees like Willows, or to convert Pines into underwood. Climatic conditions must also be taken into account in connection with these intentional mutilations of cultivated plants. To give one instance of their effect, it may be mentioned that vine-pruning in Hungarian vineyards is quite different from the corresponding process employed on the Rhine, whilst the latter again differs from the method practised in Northern Italy, which, in its turn, is not the same as that of Southern Italy. In each locality the kind of treatment most adapted to prevailing climatic conditions has been found out in course of time.

BUDS ON LEAVES.

Hitherto only such buds as are developed on roots or on the various regions of the stem have been dealt with; but an enumeration of these does not nearly exhaust the multiplicity of bud-forms which exist. Buds and shoots may also spring from the tissues of leaves—particularly foliage-leaves. These are termed epiphyllous buds or shoots, and they are classified in several groups according to their places of origin.

Before discussing this classification it is necessary to note carefully that epiphyllous buds must be strictly distinguished from those which occur on the foliage-leaves of *Helwingia* and on the leaf-like cladodes (or phylloclades) of Butcher's-broom, &c. As regards *Helwingia* (see fig. 198) careful investigations prove that certain strands proceed from the leaf-bearing axis to the buds seated upon the leaves. Each of these strands represents a lateral axis, but instead of being free it is bound up (or fused) with the midrib of the leaf from the axil of which it springs. The lateral axis thus adnate to the midrib first abandons its connection with the latter at a spot on the lamina, about a third of its entire length from the base. It there terminates in a bud, or, if it divides, in several buds, and inasmuch as these are flower-buds, it may be looked upon as a flower-stalk. These buds cannot therefore be said to be epiphyllous, *i.e.* to spring direct from the tissue of a foliage-leaf. In reality each is borne upon a structure of the nature of a stem, only the peduncle, stalk, or axis has partially coalesced with the midrib of a leaf. Willdenow, who was the first to describe it, named the plant, represented in fig. 198, the Butcher's-broom Helwingia (*Helwingia rusciflora*), because the floral buds here as in the Butcher's-broom (*Ruscus*) were borne by foliaceous structures (*cf.* vol. i. p. 333). The two cases are, however, essentially different. The green leaf-like structures in the Butcher's-broom, which carry floral buds upon their upper surfaces, are not leaves at all, but leaf-like shoots, that is to say axes, and the buds upon them are, therefore, not epiphyllous but cauline. The same statement applies, of course, to other plants with flat, expanded shoots, a few representatives of which are shown in the illustration of p. 335 of the first volume, and in this category must be included Ferns also, if we look upon their fronds as phylloclades, and not as foliage-leaves. It would be quite out of place here to enter into the question of the nature of fern-fronds, or to set forth the reasons why they must be considered as phylloclades. The proof cannot be

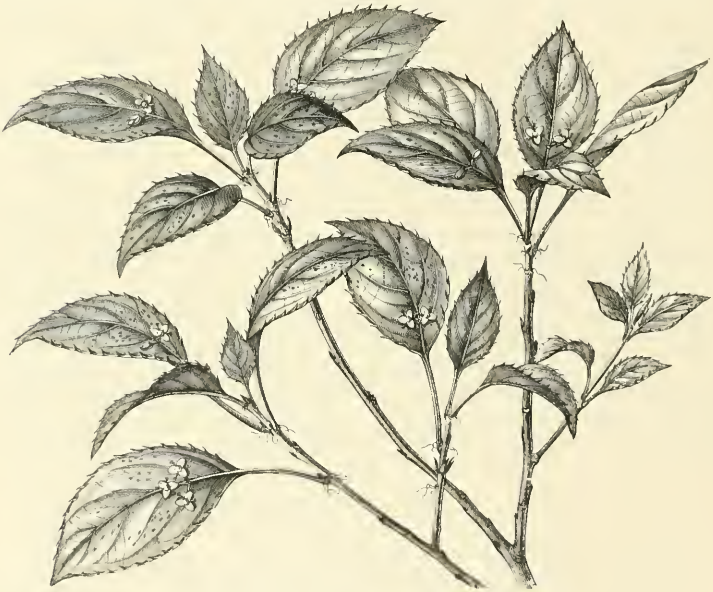

Fig. 198.—*Helwingia rusciflora*, with flowers seated upon the foliage-leaves.

conveniently introduced until we come to the description of Ferns themselves. It is sufficient to mention here that buds very frequently occur on the fronds of Ferns; indeed, certain species, *e.g. Asplenium bulbiferum* (see fig. 200) develop buds on almost all their fronds. In most cases they spring from the surface of the green pinnæ, but in *Ceratopteris thalictroides*, a common denizen of swamps in the East Indies, it is from the little stalks of the ultimate green lobes, in *Gleichenia* from the angles of the forkings of the fronds (*cf.* fig. 189 ^{6}), and in *Asplenium Edgeworthii* (see fig. 199), from the apices of the fronds, that is to say from the extremities of the cladodes. The last-mentioned Fern grows upon the bark of trees, and the tips of its fronds are endowed with the property of avoiding the light, in other words, they bend towards the darkest parts of their substratum, creeping into the fissures in the bark, where they become firmly adnate, and each develops a bud above the point of contact. This bud gives rise once more to fronds, of which, however, one only, as a rule, develops vigorously. After it has unrolled itself, this new frond in turn searches with its apex for a dark rift. The

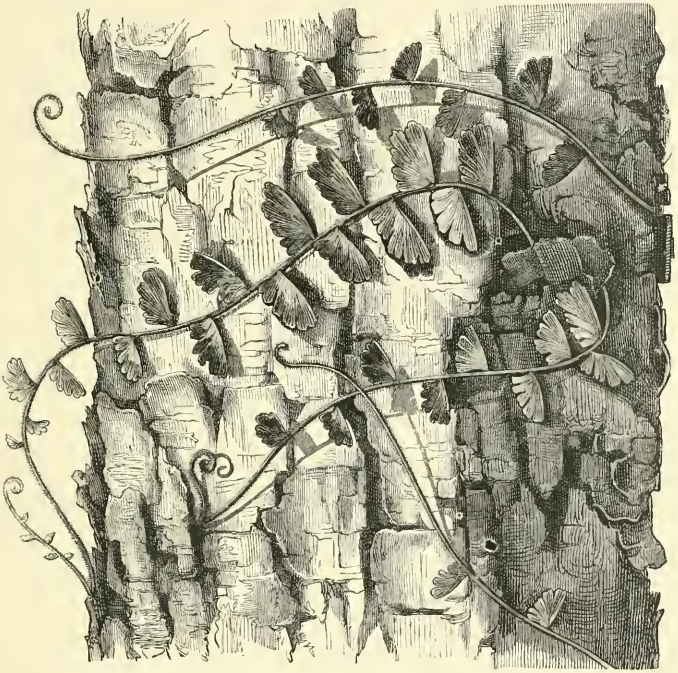

Fig. 199.—Formation of Buds on the apices of the Fronds of Ferns; *Asplenium Edgeworthii.*

process is repeated over and over again, and results in the trees, upon the bark of which the *Asplenium* has established itself, being regularly encircled and woven over by fronds, as is shown in fig. 199. The separate fronds of the fern in such circumstances have a strong resemblance to the runners of certain species of *Veronica*, *Ajuga*, and Periwinkle, which have their leaves arranged in two rows.

Unlike the above cases—viz. the buds of Helwingia borne on special stalks adherent to the leaves, those growing on the cladodes of the Butcher's-broom, and those on the fronds of Ferns, all of which must, in spite of their extreme similarity to epiphyllous buds, be looked upon as cauline—true epiphyllous buds always arise from cells of a true leaf and have no connection with adjacent axes beyond that involved in the fact of the bud-producing leaf being derived like all other leaves from a stem. Epiphyllous buds are even produced by leaves severed from the axis; indeed, in many instances, the severance of the leaves is itself the apparent cause of the development of the buds. This phenomenon is exhibited, for example, by *Bryophyllum calicinum*, a plant of the House-leek family which belongs to the tropical parts of the Old World, but has long been cultivated in our greenhouses and has attained a certain celebrity even in non-scientific circles, owing to the fact that Goethe interested himself in it and mentions it repeatedly in his writings. The foliage-leaves of this *Bryophyllum* (see fig. 200[3]) are deeply divided, the separate lobes being oblong-obovate and conspicuously notched. Every full-sized leaf exhibits in each notch of the margin a group of cells, which is perceptible as a dot to the naked eye. So long as the leaf remains upon the stem there is usually no further development of these cell-aggregates, but if the leaf is plucked off and laid on the earth an active process of division is set up in them, the result of which is the formation of a little plant with stem, leaves, and roots, as is represented in the figure opposite. The leaves of *Bryophyllum calicinum* are thick and fleshy, and contain when mature such an abundance of reserve material and water as to render it superfluous that any absorption of nutriment from the environment should take place. It is not till later that the little plants which spring from the notches of the leaf, having used up the materials stored in the latter, are driven to seek food from the environment by means of their roots. If the leaf has been laid on moderately damp earth, the rootlets of the young plants, developed in its notches, penetrate the ground and, in the event of the tissue of the leaf being in the meantime exhausted and withered, all the little plants become independent and develop into full-sized individuals. Phenomena similar to those exhibited by *Bryophyllum calicinum* are also observed in other plants with thick, fleshy leaves, particularly in Echeverias. Young plants also make their appearance sometimes on the fleshy leaves of *Rochea falcata* after they have been picked. There is, it is true, the noteworthy difference that the phenomenon is not foreshadowed, as in *Bryophyllum*, by the existence of special groups of cells at the points of origin; but *Bryophyllum*, *Echeveria*, and *Rochea* have this in common, that in all cases the need of materials for the construction of the young plants is met by the succulent leaf for some time after its severance from the stem, so that it is not necessary to place the leaf in communication with damp earth with a view to its deriving the requisite water therefrom. They are thus exempted from conditions to which the greater number of plants propagated by gardeners by means of so-called leaf-cuttings are subject.

This method of propagation by leaf-cuttings has long been recognized, and has been particularly applied to Citron and Orange trees, as also to the Wax Flower (*Hoya carnosa*), to *Theophrasta Jussieui*, a plant belonging to the Myrsineæ, to the Aucuba Laurel (*Aucuba Japonica*), to the beautiful *Clianthus puniceus*, and to various other plants besides. But it is only quite recently that it has been practised on a vast scale, since the discovery that the Begonias, introduced from the tropical parts of America and now so fashionable as ornamental foliage-plants, and the Gesneraceæ from Brazil with their splendid flowers, are capable of being propagated with extreme facility and in immense numbers by means of their leaves. The cultivator has only to pick one of the foliage-leaves and place it in contact with moist sand or sandy soil, and in a short time

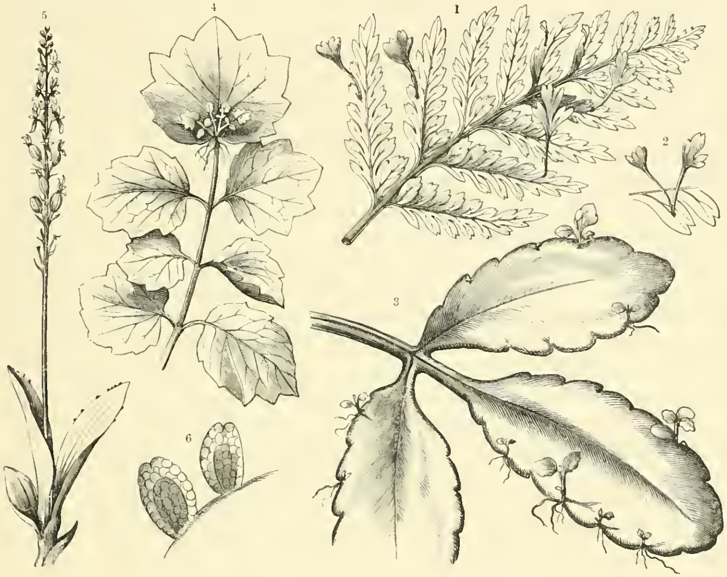

Fig. 200.—**Formation of Buds on Fronds and Foliage-leaves:**

1, 2 on the pinnules of *Asplenium bulbiferum*; 3 on the margins of the lobes of the leaves of *Bryophyllum calicinum*; 4 on the foliage-leaves of *Cardamine pratensis*; 5 on the margin of foliage-leaves of *Malaxis paludosa*. 6 Two buds on the margin of a leaf of *Malaxis paludosa*. 1, 3, 4, 5 natural size; 2 ×2; 6 ×20.

young plants sprout from the leaf and may be transplanted as independent growths. We will briefly describe what takes place.

The first change observed in a leaf which has been cut off for the purpose of forming cuttings is the desiccation of the cells lying next the cut surface. Beneath the layer of dried-up cells a cork-tissue is formed, whilst the dead, outer layer is converted into a bark. A parenchymatous tissue is next formed from the part beneath the cut which is still living; indeed, it is the epidermal cells nearest to the dead layer of cells that initiate this formation of tissue. They grow in a radial direction, elongating and dividing by means of the insertion of transverse walls, the result being a uniform thickening coextensive with the surface of the wound. A little later some of the living cells in the middle of the cut, which are still covered over by the dead layer, begin to divide; and as the tissue there grows in size, it tears the overlying dried layer into shreds and pushes it off in parts. This exuberant tissue has received the name of callus. Whilst the formation of callus is proceeding, suckers are developed at the points of contact of the leaf-cutting with the sand, their numbers being particularly abundant along the projecting ribs of the leaf. In form and function these suckers are entirely similar to the absorbent cells lying close to the growing extremities of roots, and called root-hairs. They are of the greatest importance to the leaf-cuttings in their subsequent processes of development. So long as the leaf adhered to the axis it was supplied with a sufficient quantity of water from that which was ascending through the stem; the aqueous vapour lost through evaporation was replaced by moisture absorbed by the roots from the damp soil and afterwards conducted through the stem to the leaf in question. But when the leaf has been cut off it is no longer able to derive any material from the earth through the intervention of the stem, and as its ordinary epidermal cells have not the power of taking up from the damp soil, which serves as substratum to the leaf-cutting, as much water as is lost by evaporation, the cutting is exposed to the risk of desiccation in spite of its being in contact with a wet substratum. In order to escape this danger and save itself from destruction the leaf treated as a cutting furnishes itself with absorbent cells. By their instrumentality the water, which is particularly needful for the formation of callus, is put by. Even if the materials necessary for the construction of the cells of the callus may be present in abundance in the cells of the leaf, it is of little avail unless these materials are diluted and conducted to the places where they are used up, and for this a much greater quantity of water is requisite than could be retained by the severed leaf. When the callus has reached a certain size numerous roots make their appearance. They usually take their rise from cells of the parenchyma adjacent to a vascular bundle of the leaf, break through the callus, and grow rapidly in length. Only after the development of these roots, which absorb liquid copiously from the substratum by means of their suction-cells, are buds produced on the upper—less frequently also on the under—surface of the leaf-cutting. In Begonias it is chiefly cells of the epidermis that give rise to buds; in other plants, particularly in the Gesneraceæ, in the species of *Peperomia*, a genus belonging to the Pepper order, in *Tournefortia*, *Citrus*, &c., it is cells of the callus that divide and become the rudiments of buds, and indirectly of shoots. In the case of Begonias isolated buds occasionally spring from the callus in addition to the others, but this is not inconsistent with the fact that in these plants the epidermal cells are the favourite places of inception. Especially are those epidermal cells preferred which are situated above the bifurcation of a vascular bundle in the lamina. If an entirely uninjured leaf is laid upon moist sand, the buds develop just above the base of the lamina where the strands radiate out from one another. It is a common custom of gardeners, however, when making use of Begonia-leaves to propagate the plant, to set the petiole in wet sand and to make a number of transverse cuts across the larger veins of the lamina, which is laid flat upon the sand. After this operation quite a host of buds—*i.e.* new plants—take their rise all along the course of the intersected vein, some immediately in front of the cut, which is covered by a callus, but frequently others again at a distance from that spot. From this we may conclude that the new formation depends principally upon the conduction of material by the veins. No doubt its relative position with regard to the roots developed from the callus to the stock of reserve materials and so forth, also play an important part. The upshot is, however, that numberless cells of the epidermis of the leaf become the seats of inception of new plants, and that buds are able likewise to develop from deeper-lying cells of the callus. Whether the development of an epiphyllous bud has begun in one place or another, there is always in the inceptive area a concomitant production of vascular bundles, which establish a connection between the axis of the bud in process of formation and the previously-developed roots; and it is not long before the axis produces green foliage-leaves capable of assimilating in the presence of light. The leaf-cutting, upon which a miniature plant is now seated, in most cases retains its vitality for a considerable time longer, but at length it begins to turn yellow and gradually it dies. Only that part which produced the buds and roots persists in the form of a pad, forming in some species, for example, in Begonias, a thick, fleshy, cellular body, looking almost like a little tuber.

The phenomenon above described as ensuing in consequence of artificial manipulations takes place sometimes spontaneously in nature in a few plants, and that without the leaf concerned in the process being separated from the axis. Examples of plants which have been observed to bear occasional epiphyllous buds when growing wild in their natural habitats are Cruciferæ (*Cardamine pratensis*, *Nasturtium officinale*, *Roripa palustris*, *Brassica oleracea*, *Arabis pumila*), Papaveraceæ (*Chelidonium majus*), Water-lilies (*Nymphæa guianensis*), Gesneraceae (*Episcia bicolor*, *Chirita sinensis*), Lentibularieæ (*Pinguicula Backeri*), Aroideæ (*Atherurus ternatus*), Orchidaceæ (*Malaxis monophyllos* and *M. paludosa*), Liliaceæ (*Fritillaria*, *Ornithogalum*, *Allium*, *Gagea*, *Hyacinthus*) and Amaryllideæ

(*Curculigo*). In many cases the buds which arise in the form of little papillæ grow straightway into miniature plants, as in the case of the Cuckoo-flower (*Cardamine pratensis*, see fig. 200 [4]), or else little bulbs are formed in the first instance, as in the various species of Garlic and in the Crown-imperial (*Allium* and *Fritillaria*), or small tubers, as in the above specified instances of the genus *Malaxis*. In the one case cells situated in the middle of the lamina—usually above the point of bifurcation of a vascular bundle—are the seat of origin of buds, as, for example, in the Cuckoo-flower, already so often referred to; in other cases, such as *Curculigo*, the buds spring from the extremity of the midrib. The little orchid *Malaxis paludosa* (see fig. 200 [5]), which is a native of moorlands in North-western Europe, develops its diminutive buds principally on the surface and margins of the upper portions of the green foliage-leaves, and these buds appear in such large numbers that several botanists state in their descriptions that the leaves of *Malaxis paludosa* are for the most part "shortly ciliated". Of all the manifold kinds of epiphyllous leaves these little structures produced on the green leaves of the Orchid in question possess a surpassing interest on account of their form. Each bud (two of which are shown in fig. 200 [6]) consists of a yellowish-green cellular body, shaped like a kernel, and of a layer of cells hanging loosely together and enveloping the kernel like a sac. At the free extremity the cells of the envelope form a kind of ring, which constitutes the rim of a round depression. The resemblance of these buds to the seeds of Orchids, especially to those of *Malaxis paludosa*, is obvious on the most cursory examination, and it will again be referred to in a subsequent section.

Buds are found much less frequently on scale-leaves and floral-leaves than on the green foliage-leaves. Sometimes they may be observed to spring from bulb-scales if the latter are stripped off the axis and put into moist sand. In these cases they are invariably developed at the spots where the scales have been cut and injured. Dutch cultivators of bulbs make use of this property to propagate hyacinths direct from the bulb-scales. They cut out the axis of the bulb, remove also any rudiments of floral axis which may be present, and cut transversely through the lower part of the bulb-scales. Not infrequently the bulb-scales are also partially divided longitudinally. One would think that after such treatment the bulb must sooner or later perish; but, on the contrary, a crowd of small bulb-like buds are produced on the scales at the edges of the cuts, and cases are known of over a hundred young bulbs being obtained in the manner described from the scales of a single hyacinth bulb.

Of all epiphyllous buds those originating in the tissue of floral-leaves are, as stated, the least common. Minute buds have, however, been repeatedly observed to be developed, instead of seeds, on the carpels in the interior of the fruits of several species of *Crinum* and *Amaryllis*. They were seated on round bodies of tissue, which were not distinguishable from little tubers. When laid on damp soil, each produced a new plant. We need only allude here to the cases of parthenogenesis, which will be discussed later on, wherein seeds capable of germinating are developed without fertilization from the ovules concealed in the ovary.

The instances of bud-formation above enumerated, when considered with respect to their origin, show that not only cells of roots, but also those of all regions of the stem, and of scale-, foliage- and floral-leaves may become initial cells of buds, or, in other words, of rudimentary shoots. Hence we may draw the conclusion that all the living protoplasts which are capable of division in whatever part of the plant their cells are situated, from the root-tip to the highest apex of the stem, and from the scale-leaves to the ultimate floral-leaves, have the power of undertaking the function of renovation without previously undergoing fertilization. Under ordinary circumstances, no doubt, it is only protoplasts in the cells of the axis, close to the spots where the foliage-leaves emerge, which turn into rudiments of shoots, and the most natural explanation of the selection of these places is that the constructive materials prepared or temporarily deposited in the foliage-leaves may there be turned to account at first hand; but in extraordinary circumstances—*i.e.* as a consequence of unfavourable climatic conditions, or of dangerous injuries, and particularly under the influence of approaching peril of death—the important task of initiating new plants devolves also upon cells situated at most widely different parts of the parent stock, cells which otherwise would certainly not have assumed this function. In these cases it is astonishing to see how stress of external circumstances results in an entirely new division of labour in the cells of the tissue affected thereby; how in one place a protoplast, originally destined to play an altogether different part, divides and becomes the starting-point of a fresh plant, whilst the protoplasts of neighbouring cells convey constructive materials to that particular member of their fraternity and are regularly consumed by it. Very different would have been the order of things and the kind of co-operation of adjoining protoplasts under ordinary conditions!

2. REPRODUCTION BY MEANS OF FRUITS.

Definition and Classification of Fruits.—Fertilization and Fruit-formation in Cryptogams.—The Commencement of the Phanerogamic Fruit.—Stamens.—Pollen.—Arrangements for the Protection of the Pollen.—Dispersion of Pollen by the Wind.—Dispersion of Pollen by Animals.—Allurements of Animals with a view to the Dispersion of Pollen.—The Colours of Flowers considered as a means of attracting Animals.—The Scent of Flowers considered as a means of attracting Animals.—Opening of the Passage to the Interior of the Flower.—Reception of flower-seeking Animals at the entrance to the Flower.—Taking up the Pollen.—Dispersion of the Pollen.—Cross-pollination.—Autogamy.—Fertilization and Fruit-formation in Phanerogams.

DEFINITION AND CLASSIFICATION OF FRUITS.

To all appearance there is no difference between the protoplasts which develop into brood-bodies and those which are the points of origin of fruits. Nevertheless, it has been ascertained by experience that the protoplast, which is the starting-point of a brood-body, evolves its constructive energy without receiving any special stimulus from the protoplasm of a second cell of distinct origin, whereas for the development of a fruit the necessity of such a stimulus is a characteristic and distinctive feature of the phenomenon. Brood-bodies may spring from any part of a plant. If the parent-stock as an individual is in danger of perishing, brood-bodies are developed from protoplasts which otherwise would never have been called upon to play such a part. Brood-bodies may develop on roots, stems, and leaves, on foliaceous prothallia, and on hyphal filaments. They may be formed above or below the ground, and upon or beneath the surface of water. Their origin may be from superficial cells or from cells deeply seated in a tissue. It is scarcely going too far to say that in cell-aggregates of large dimensions the protoplasm of every young cell is potentially the starting-point of a brood-body.

If a fruit is to arise, the *ooplasm, i.e.* the protoplasm destined to initiate a new generation, must unite with the fertilizing protoplasm, which is called *spermatoplasm*. The two protoplasts concerned in this phenomenon originate at separate spots, and if they are to coalesce the space between them must be surmounted. One at least of the two protoplasts must accomplish a change of place, and this locomotion must take place in a definite direction. The union of two protoplasts which have been formed at places separated in space from one another constitutes the essence of the process of fertilization, and it results in a change in the ooplasm which, in accordance with our idea of the minute structure of the substances in question, may be looked upon as a displacement of molecules and an alteration in their grouping. Sometimes this internal rearrangement is plainly manifested externally by a change of form and colour, or by an increase in size; and where this occurs it ensues immediately upon fertilization. But for the most part no alteration in the fertilized ooplasm is perceptible at first, and it would be difficult to specify any certain signs whereby the fertilized ooplasm may be distinguished from the unfertilized. It is, however, known by experience that in most cases the unfertilized ooplasm dies without developing further, whereas the fertilized ooplasm, after a longer or shorter period of rest, exhibits a characteristic growth and becomes the point of origin of a young organism, the new generation. The ooplasm rendered capable, by fertilization, of this particular kind of growth is to be considered as an *embryo*, even in cases where no outwardly-visible change in form, size, or colour has taken place.

Both ooplasm and spermatoplasm are formed in special cells at definite spots on a plant which is preparing to reproduce itself by means of fertilization. The cell-chamber wherein the ooplasm is developed, and which is itself adapted to the reception of foreign matter, and constitutes the point of origin of the embryo, will in future be called an *oogonium* (ᾠόν = egg; γόνος = parentage); the cell wherein the spermatoplasm is brought to the proper form and composition for the purpose of fertilization is called an *antheridium* in the case of a Cryptogam, and a *pollen-grain* in the case of a Phanerogam. In a few instances the ooplasm is set free from the oogonium and fertilized outside it; the oogonium has then, of course, nothing more to do with the subsequent processes of development. In other cases fertilization takes place within the oogonium; the oogonium persists in a more or less altered form as the immediate envelope of the embryo, and is then designated by the name of "carpium" (καρπός = fruit), or briefly "carp". In yet other instances it is possible, at the very earliest stages of development, to distinguish a special multicellular envelope surrounding the oogonium. To this envelope we may apply the term "amphigonium" in order to simplify the terminology. If the amphigonium is later on converted into the coat of the carpium, it may be called an "amphicarpium". In many plants this envelope to the oogonium is succeeded externally by a second called a "pericarpium", which will be the subject of more detailed study later on.

Now what ought we to take to be the fruit? To try to conform to ordinary usage, or to adopt the terms employed in other sciences, would cause fatal confusion. The most expedient course, therefore, seems to be to put aside the names and definitions adopted in other departments and to lay down an independent and unambiguous definition of the plant-fruit, and apply it to all plants. Thus, from the botanical point of view, *we consider every structure to be a fruit which is the product of fertilization, and at the same time constitutes the first step towards the renewal of the fertilized plant.* This definition includes the ooplasm, which is fertilized outside the oogonial envelope, and forms the starting-point of a new individual; there may, therefore, be fruits each consisting of nothing more than an embryo. But usually the ooplasm is enveloped by a coat, which may be single or double, or even threefold. Fertilization then takes place within these coverings, and the influence of the spermatoplasm extends more or less beyond the ooplasm to its investments. In such cases the coats also are involved in the process of fruit-formation. They are stimulated to grow in a particular manner and take the form of a mantle clothing the embryo, of a protective cover, or of some contrivance which promotes the further development of the embryo and its full expansion into a new generation. Fruits of this kind have sometimes a very complicated structure. In them we are able to distinguish a complex outer coat, and within, the embryo with its tightly adherent covering, the latter portion of the fruit being that which has from ancient times borne the name of *seed*. Fruits thus come before us as a series of forms, of which the members at opposite extremities of the series differ greatly, but are linked together by a large number of intermediate forms. At one end of the chain we have the unicellular fruits of the microscopic Desmids, at the other the fruits of the Cocoanut, which is differentiated into seeds on the one hand and several envelopes on the other, and is as large as a man's head.

As already stated, the spermatoplasm acquires the composition and form whereon its fertilizing power depends within the confines of certain special cells. Extreme variety is, however, found to prevail in this connection. In some plants, especially those which conduct the process of fertilization under water, the spermatoplasm takes the form of minute particles usually furnished with special motile cilia to enable them to swim about. These have received the name of *spermatozoids*. They escape from the cell-chambers in which they were formed into the water, rush about for a short time or are carried by currents in the water, and finally reach the ooplasm, whereupon they place themselves in contact with it, and enter into combination with it in a manner which may best be likened to the merging together of two drops of oil floating upon the surface of water. In another category of plants the spermatoplasm does not escape from the cell in which it has been developed, but this cell itself enters into combination with the oogonium as a whole, and a possibility is afforded in a variety of ways for the two kinds of protoplasm to coalesce within a single enveloping cell-membrane. A third category of plants is remarkable for the fact that the spermatoplasm does not coalesce as a whole with the ooplasm, only a portion of it passing to the ooplasm.

The above prefatory remarks give some idea of the extreme variety which exists in the processes of fertilization, and it is no easy matter to give a short and concise, and at the same time accurate, presentation of the facts involved, especially if one tries not to use more than is absolutely necessary the innumerable technical terms invented in recent times. Even taking into account only the most important of the phenomena above referred to, we find twelve different processes or types of fertilization and fruit-formation, and it will be the object of the next chapter to present these in order, beginning with the simplest cases and concluding with the most complicated.

It will materially conduce to clearness of exposition if, in considering these phenomena, we adhere to the old classification into *Cryptogams* and *Phanerogams*, which was introduced by Linnæus. According to the etymology of the words, Cryptogams are plants which are fertilized secretly, whilst in Phanerogams the process of fertilization is apparent. Since the microscope has been perfected and brought into common use this distinction has no doubt lost its significance. If, however, we adopt a somewhat different interpretation of these terms, we may continue to use them with advantage. Thus, under the name of Cryptogam we shall include all plants destitute of flowers in the ordinary sense and possessing organs of fructification which are not clearly visible excepting under the microscope, whilst the term Phanerogam will comprise such plants as bear flowers, and have organs of fructification which are visible without aid from the microscope and are of the nature of metamorphosed leaves. The retention of these old and familiar terms is rendered all the more desirable by the fact that another important distinction, which is inherent in the process of fertilization itself, and has not as yet received sufficient attention, is involved in the separation of Cryptogams and Phanerogams, namely, that in Cryptogams fertilization takes place in water or in a watery medium, whereas the process in Phanerogams is accomplished almost exclusively in the air.

FERTILIZATION AND FRUIT-FORMATION IN CRYPTOGAMS.

In the mountain districts of Central Europe, after the winter snow has melted and the turbid water derived from it has gradually cleared itself up, a beautiful sight is afforded, especially when a ray of sunshine strikes the water, by the dense crowds of short delicate filaments of a bright emerald-green colour, which everywhere form a coating to the stones at the bottom of streams and to the sides of the troughs used to convey spring-water from the heights. These green threads belong to a plant named *Ulothrix*. Each separate filament consists of numerous cells joined together so as to form a chain, as is shown in fig. 201 1. When these filaments are mature, and the time has come for the production of fruit, the protoplasmic contents of the separate cells break up into a number of spherical green masses, which, however, continue to be held together in a rounded cluster by means of a colourless substance. An aperture is now formed in the wall of each of the cells in question, and through this opening the conglomerate mass escapes into the surrounding water (see figs. 201 2 and 201 3). The individual masses of protoplasm which compose the conglomerate are set free shortly afterwards, and each exhibits at its anterior extremity a pair of revolving cilia, by means of which it swims about in the water (fig. 201 4). When in the course of their peregrinations two protoplasts which originated in one and the same cell-cavity encounter one another they get out of each other's way; if, on the other hand, the protoplasts from cells belonging to different filaments meet, far from avoiding one another, they come into full collision with their anterior ciliated extremities, turn over, and lay themselves side by side and coalesce, forming a single body with four cilia (see fig. 201 5). A little later the cilia vanish, and the product of the coalescence comes to rest. This fusion is the simplest conceivable case of fertilization in the whole realm of plants. The product of fertilization is the fruit. It consists in *Ulothrix* of the little lump of protoplasm formed by the process of coalescence just described, which now surrounds itself with a thick cell-membrane, and fastens on to some stationary body under water (see fig. 201 6). We have nothing to do at present with the subsequent development of this fruit; it is sufficient to remark in order to explain the illustration that the attached unicellular fruit does not produce again immediately a string of cells, but that first of all swarmspores are developed from its protoplasm (see figs. 201^{7} and 201^{10}), and these fasten on to appropriate spots, inclose themselves in cell membranes, divide and ultimately initiate new filaments composed of cells arranged in linear series as before.

In *Ulothrix* and allied genera the protoplasts which pair as a first step to the formation of fruit do not differ from one another in form, size, colour, or mode of locomotion, and it would be impossible to determine from outward appearances which of them acts as fertilizer and which is fertilized. The terms *ooplast* and *spermatoplast* are therefore not applied to them, but they are called *gametes*, and the entire process described in connection with them may be spoken of as *fruit-formation by pairing of gametes.* This process of pairing is, so far as it can be apprehended by our senses, a mutual permeation of the two protoplasmic bodies, and we may suppose that a rearrangement of molecules is caused thereby, which endows the product of pairing with the power of developing independently. This assumption is supported in particular by the fact that if any gametes, after being set free from the conglomerate, fail to pair they undergo no subsequent development but deliquesce in the surrounding water and perish.

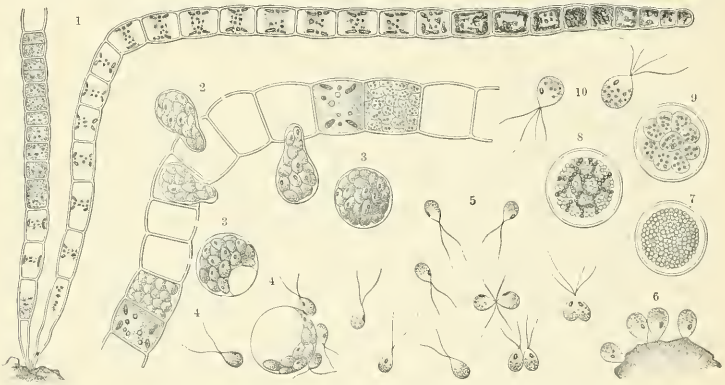

Fig 201.—Fertilization and fruit-formation in *Ulothrix zonata* (partly after Dodel-Port).

^{1} Two filaments composed of cells joined together in chains. ^{2} Escape of conglomerated gametes. ^{3} Spherical conglomerate of gametes after it has escaped. ^{4} Separation of the gametes. ^{5} Gametes swimming about and pairing. ^{6} Fruits (products of the pairing of gametes) attached to a substratum. $^{7-9}$ Subsequent development of fruit. ^{10} Two swarmspores produced by fruit. ^{1} × 250; $^{2-10}$ × 400.

The Wracks or Fucaceæ, which grow profusely in the sea, resemble *Ulothrix* inasmuch as the protoplasts, destined to act as fertilizers, escape from their cell-cavities, fertilization consisting of a fusion of free protoplasts disconnected from the mother-plant. But these Wracks differ very strikingly from *Ulothrix* and allied forms in that the protoplasts are of two kinds, there being an obvious diversity in size and form between ooplasts and spermatoplasts. The thallus in all species of *Fucus* is tough and leathery, brown in colour, foliaceous, and dichotomously branched or lobed, and has interspersed here and there air-containing swellings which serve as floats. The apices of the lobes are punctate, and each spot corresponds to an internal cavity which has the form of a globular pit (see fig. 202[1]). Sections through these cavities show that a large number of segmented filaments known as "paraphyses" spring from the lining-layer of the cavity. In *Fucus vesiculosus* (figs. 202 and 203) these filaments remain concealed in the cavity; in some other species of *Fucus* they protrude through the narrow orifice (ostiole) of the cavity in the form of a pencil of hairs. Amongst the filaments other structures are also formed within the cavity. A few of the cells lining the cavity swell into papillæ, and each becomes divided by the intercalation of a transverse septum into two cells, one of which is spherical, whilst the other assumes the form of a stalk bearing the upper one (see fig. 202[2]). The protoplasm in the spherical cell is dark brown, and breaks up into eight parts, which round themselves off and constitute the ooplasts. The thick wall of the spherical cell resolves itself into two layers, of which the inner one incloses the eight rounded protoplasmic bodies like a bladder. This bladder stuffed full of ooplasts next detaches itself entirely, and glides upward between the paraphyses until it reaches the orifice of the cavity.

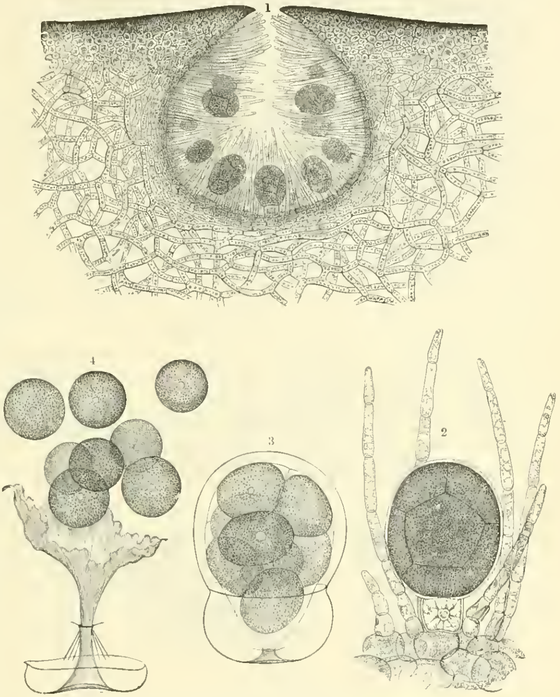

Fig. 202.—*Fucus vesiculosus.*

[1] Longitudinal section through one of the cavities in the thallus. [2] A vesicle surrounded by paraphyses from the bottom of the cavity. [3] A detached vesicle containing eight ooplasts; the inner lamella swollen up. [4] Liberation of the ooplasts from a rent vesicle. (After Thuret.)

Here the bladder splits into two lamellæ, and finally the inner lamella becomes inflated, bursts and shrivels up, leaving the eight ooplasts free (see figs. 202^3 and 202^4).

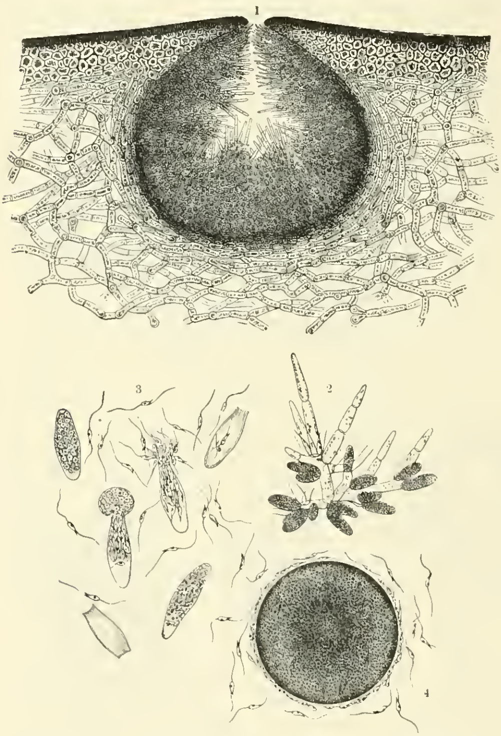

Fig. 203.—*Fucus vesiculosus.*

^{1} Longitudinal section through a portion of a thallus including a cavity full of antheridia. ^{2} Antheridia extracted from a cavity of the kind. ^{3} Spermatozoids escaping from the antheridia. ^{4} Spherical ooplast covered with spermatozoids $^1\times 50$; $^2\times 160$; ^{3}, $^4\times 350$. (After Thuret.)

Whilst a certain proportion of the individual plants of *Fucus vesiculosus* develop ooplasts in the cavities in their lobes, other individuals give rise to spermatozoids in similar cavities (see fig. 203^1). The cells lining the hollows develop papillose protuberances which grow longitudinally, divide and form a ramifying mass of cells as is shown in fig. 203^2. Here and there the extremities of branches in this mass of cells have a dark brown colour, and their protoplasmic contents are broken up into a number of minute portions (the spermatozoids). These vesicles become detached and collect at the orifice of the cavity. This happens especially at the time when that zone of the sea-shore where the wrack grows is left dry, and the *Fucus* plants are lying flat upon the stones, and look like brown and faded leaves. At the recurrence of high-tide, when the wracks are again submerged, the cells full of spermatozoids burst, and the tiny spermatozoids formed from their protoplasmic contents swarm out into the surrounding water. Each spermatozoid has a sharp and a blunt end, exhibits a so-called eye-spot, and is furnished with two long cilia by means of which it swims about in the water (see fig. 203^3). Analogy to similar processes which take place in Mosses makes it seem probable that the ooplasts above described as lying near the orifices of cavities in the thallus secrete some compounds or other—presumably organic acids—which attract the spermatozoids swarming in the water. The actual fact is that spermatozoids which come into the vicinity of the spherical ooplasts adhere to them in such large numbers that a sphere is sometimes entirely coated with spermatozoids (see fig. 203^4).

It has also been observed that the spherical ooplasts are set rolling by the adherent spermatozoids, and are thus removed from the places where they previously lay stranded. The fertilizing effect exercised by the spermatozoids, one of which, as it appears, coalesces with the ooplasts, consists doubtless in a rearrangement of molecules, and the first outwardly visible result of this rearrangement is the envelopment of the ooplast in a tough cell-membrane. The body must now be considered to be a fruit—a unicellular fruit, which remains unaltered in a state of rest for some time, but at length bestirs itself, and stretching out attaches itself firmly to the ground by means of root-like outgrowths. It then divides and gradually develops into a fresh *Fucus* plant.

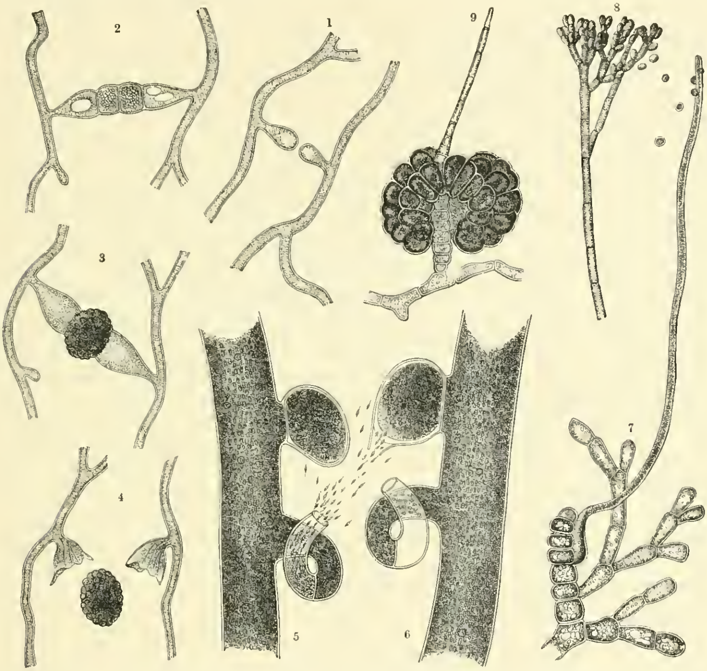

Fig. 204.—Fertilization and Fruit-formation in *Mucorini*, *Siphonaceæ*, and *Florideæ*.

$^{1-4}$ Conjugation and fruit-formation in *Sporodinia grandis*. ^{5}, ^{6} *Vaucheria sessilis*. ^{7} Fruit-rudiment with trichogyne of *Dudresnaya coccinea*. ^{8} Antheridia of the same plant with spermatozoids in the act of abjunction. ^{9} Fruit of the same. $^{1-4}$×180; ^{5}, ^{6}×250; ^{7}, ^{8}×400; ^{9}×250. ($^{7-9}$ after Bornet.)

In the two cases just described, the ooplasts are not fertilized till after they have escaped from the cells of the mother-plants into the surrounding water, and at the time of fertilization they are destitute of any special coverings of their own. In the plants to be dealt with next, on the other hand, the ooplasts at the time of fertilization are still in connection with the mother-plant. The cell-membrane, which maintains this union, persists as an envelope to the protoplasm which is to undergo fertilization. There are two ways in which a fertilizing protoplast may exercise its influence upon a protoplasmic body thus inclosed in a cell-membrane. Either a piece of the envelope is broken through and a free passage made for the spermatoplasm to the ooplasm, or else, if a true fertilization takes place, it must be by osmosis through the envelope.

The solution and removal of part of the cell-membrane enveloping the ooplast, and the opening up of a passage in which the spermatoplast can unite with the ooplast, is observed to occur in the Mould-fungi known as *Mucorini*, and also in the innumerable little green and brown water-plants which, on account of their characteristic mode of fertilization, have received the name of *Conjugatæ*. In these plants the coalescence of the two kinds of protoplasts is always preceded by a process of "conjugation", that is to say, the envelopes surrounding those protoplasts come in contact and grow together, and a special cavity is thereby created in which the fusion of the protoplasts can take place. This method of fertilization is shown in the clearest manner in fig. 204^{1,2,3,4}, the instance being that of *Sporodinia grandis*, a Fungus belonging to the *Mucorini*. Two more or less parallel tubular hyphæ put forth lateral protuberances (fig. 204^{1}) which stretch out towards one another until their free ends come into contact and cohere. As soon as this union is effected, a transverse wall is formed on either side of the plane of contact, and it is now possible to distinguish in the limb connecting the two hyphæ a median pair of cells supported by the two basal portions of the outgrowths (see fig. 204^{2}). The connecting limb is usually likened to a yoke (ζυγόν). The wall arising from the junction of the outgrowths, and now separating the two cells in the middle of the yoke, dissolves, thus producing a single cell-cavity (instead of the two), which is called a "zygogonium". The two protoplasts inhabiting the pair of cells were hitherto separated, one being derived from the hypha to the right, and the other from the hypha to the left; they are two different individuals, but, upon the dissolution of the wall between them, they coalesce within the zygogonium. This coalescence is to be looked upon as the act of fertilization. The membrane of the median cell, which surrounds the blended mass of protoplasm, thickens, and, in the selected instance of *Sporodinia grandis,* becomes warted, whilst in *Mucor Mucedo* (fig. 193^{3}) it becomes rough and wrinkled, and in other *Mucorini* even spinose. It also acquires a decided dark coloration. Lastly, the dark median cell detaches itself from the basal portions of the original outgrowths, which have held it up to that time, and thus becomes free and independent (see fig. 204^{4}). It then drops just as a cherry does from the twig of a tree, and, like the cherry, it must be designated as a fruit, although it consists of a single cell only. Fruits of this kind have received the name of "zygotes".

It is no more possible to say which of the two protoplasts uniting in the zygogonium of *Sporodinia grandis* is fertilized and which acts as fertilizer, than it is to predicate of the pairing protoplasts of *Ulothrix*, that the one is the ooplast, and the other the spermatoplast. Theoretically we must assume there is a difference, and it probably consists in peculiarities of molecular constitution, but no perceptible difference can be detected in size, configuration, or colour, nor is there any apparent distinction in respect of origin.

In the *Desmidiaceæ* also, of which two examples (*Closterium* and *Penium*) are given in vol. i. Plate I. figs. *i* and *k*, and in the *Diatomaceæ*, whose species are reckoned by hundreds, no perceptible external difference exists between the protoplasts which unite for the purpose of fertilization. Only in the *Zygnæmaceæ* is it possible to look upon a particular one of the combining protoplasts as an ooplast, and the other as a spermatoplast, and the distinction is in this case founded on their relative positions. An instance of the mode of fertilization prevailing in these plants is shown in Plate I. fig. *l*, in the first volume, the case chosen for illustration being that of *Spirogyra arcta*, which consists of green filaments of a slimy consistence, and occurs very commonly in our ponds. The cells are arranged in linear series, and from some of them are formed lateral outgrowths like those produced by the tubular cells of *Sporodinia grandis*. As in *Sporodinia*, the outgrowths from opposite cells come into contact, coalesce, and form a kind of yoke. Usually a number of the opposite cells of two filaments floating close together in the water establish connecting links of the kind, which resemble the rungs of a ladder (see vol. i. Plate I. fig. *l*, to the right). The wall formed by the coalescence of the two apices of the outgrowths is removed by solution, and a channel connecting the opposite cell-chambers of the *Spirogyra*-filaments is thus opened up. In the meantime the protoplasm in each of these cells undergoes a change. Hitherto it has been occupied by a chlorophyll-body in the form of a spiral band, but now it assumes the form of a dark-green spheroidal mass, which is destined to unite with the one opposite to it. In *Spirogyra* this coalescence does not take place in the middle of the connecting canal as in *Mucor* and *Sporodinia*, but the green ball of protoplasm from one cell glides through the transverse passage into the opposite cell-chamber, and there coalesces with the second protoplasmic mass which has remained at rest and not changed its position. It is permissible to call the resting protoplast an ooplast, and the one which moves across to it a spermatoplast; but it must again be expressly stated that in *Spirogyra* no difference in size, shape, or colour can be detected between the two uniting protoplasts. It is worthy of note that the zygote produced by the coalescence, and now assuming an ellipsoidal shape, is not equivalent in bulk to the two protoplasts, as one might expect, but that its volume is obviously smaller. We may infer from this that at the moment of coalescence a fundamental change in the molecular structure of the entire mass takes place. The characteristic property of fertilization in the *Conjugatæ*—of which *Sporodinia grandis* and *Spirogyra arcta* have here been chosen as examples—consists in the union of two separate individuals by means of the formation of a yoke between opposite cells which put forth lateral outgrowths towards one another for the purpose; this is the reason why this kind of fertilization is called conjugation, and the plants concerned are named *Conjugatæ*.

Similar to conjugation, but differing from it in several essential particulars, is the mode of fertilization by means of a protruding outgrowth from the antheridium, which pierces through the wall of the oogonium. This method is observed to occur in particular in the destructive parasites comprised under the name of Peronosporeæ. The species named *Peronospora viticola*, which is represented in fig. 205, has attained a melancholy notoriety as a parasite on the Vine, and to the same group belong *Peronospora infestans*, which causes the Potato-disease, *Cystopus candidus*, known as a deadly parasite on Cruciferous plants, the various species of *Pythium*, &c. Tubular hyphæ develop directly from the spores of these Peronosporeæ, which attack the fresh foliage, green shoots, or young fruits of the particular flowering plants that they select to serve as hosts. The hyphæ bore into the green tissue, piercing through the cell-walls and growing in the intercellular spaces, where they ramify extensively. Segmentation of the hyphæ by the introduction of partition-walls is comparatively rare, but very frequently little suckers, called "haustoria", are sunk into the interior of the living cells of the host (see vol. i. p. 165, fig. 32[1]). These hyphæ infesting the green tissues of the host-plant swell up at their blind extremities into globular heads, and a septum is introduced in each case to partition off the terminal sphere from the rest of the tube, which preserves its cylindrical form. The spherical cell is an oogonium, and the protoplasm forming its contents is the ooplasm. The latter differentiates itself into two portions, namely, a central darker ball and a clearer transparent enveloping mass. The antheridia containing the spermatoplasm develop in the form of lateral clavate outgrowths from another tube, or more rarely from the same tube. These protuberances grow towards the oogonium and apply themselves to its surface. As soon as the antheridium touches the oogonium it sends out from the point of contact a conical or cylindrical hollow process which pierces the wall of the oogonium and penetrates to the dark ball in the middle of the ooplasm (see fig. 205[3]). Meanwhile the protoplasm in the antheridium has differentiated itself into a parietal lining on the one hand and the true spermatoplasm on the other. The antheridial process, which has received the name of "fertilizing-tube", opens at the extremity buried in the interior of the oogonium; within an hour or two the spermatoplasm has flowed through this channel to the ooplasm and become so completely merged with it that it is no longer possible to recognize any boundary between the two. A short time afterwards the fertilized ooplasm incloses itself in a thick cell-membrane composed of several layers. The outermost layer is usually rough and warty, and in some species is even beset with spikes. The fruit thus formed is unicellular and remains so. It frees itself from the now decaying oogonium—thus effecting its separation from the mother-plant—and then enters upon a long period of rest. The new generation developed from the fruit begins as a tube which subsequently, in some cases, puts out sac-like processes and branches and fashions itself into the likeness of the mother-plant without passing through any intermediate stage; or in others, the tube, which represents the embryo, produces first of all from its protoplasm a number of swarmspores. These roam about for a period and then seek out a convenient spot where they come to rest and develop into new individual plants. The additional production by Peronosporeæ of spores on dendritically-branched hyphæ growing out through the stomata of the green host-plants is shown in fig. 205^{2}, but an opportunity will occur later on of discussing the details of that process.

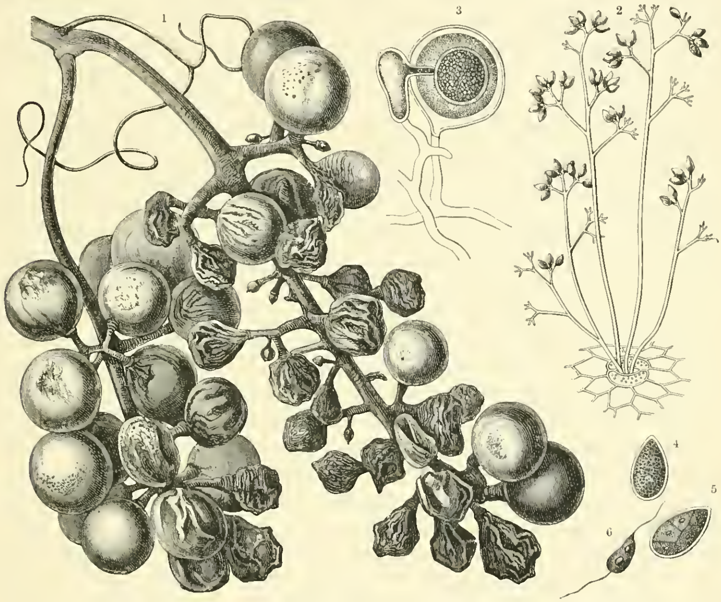

Fig. 205.—Fertilization, fruit-formation, and spore-formation in the Peronosporeæ.

^{1} A bunch of grapes attacked by the Vine-Mildew. ^{2} Spores on branched stalks projecting through a stoma of a Vine-leaf ^{3} Fertilization in *Peronospora viticola*. ^{4} A single spore. ^{5} A single spore the contents of which are dividing into swarmspores. ^{6} A single swarmspore. ^{1} natural size; $^{2}\times 80$; $^{3-5}\times 350$; $^{6}\times 380$. ($^{3-6}$ after De Bary.)

The Siphonaceæ exhibit a different mode of fertilization from those processes which involve the preliminary construction of a fertilization-tube and a conjugation-canal respectively. All the Siphonaceæ live in water or on damp, periodically submerged earth; they contain chlorophyll and are neither parasites nor saprophytes. We may take as a type of this group of plants, which includes forms of great diversity, a species of the genus *Vaucheria* (see vol. i. Plate I. fig. *a*, and text p. 23) and use it also to illustrate the processes about to be considered.

If a green filament of *Vaucheria* is examined under the microscope it is found to consist of a single tube without septa, but with numerous saccate branches. The sac-like outgrowths serve a variety of purposes; those at the base fasten the tube to the substratum, those at the free extremity develop swarmspores, whilst those springing laterally from the filament have the functions of fertilization and fruit-formation. The lateral outgrowths are of two kinds (see figs. 204 [5] and 204 [6]). One form is short, thick, and oval, and usually projects obliquely; the other is a slender cylinder curved like a chamois horn or wound round in a spiral, and sometimes it is subdivided into several little horns. The protoplasm in these sacs severs itself from the protoplasm of the main tube and a partition of cellulose is inserted in the plane of disjunction in each case. We have thus corresponding to each protuberant sac a cell-cavity or receptacle which incloses the protoplasm destined to take part in the formation of fruit. The obliquely-oval receptacles contain ooplasm and are oogonia, the curved, cylindrical receptacles inclose spermatoplasm and are antheridia. Their development is accomplished rather rapidly. It usually commences in the evening, and by the following morning the oogonia and antheridia are already completed. During the course of the forenoon an aperture appears at the apex of the oogonium, whilst simultaneously the ooplasm within it contracts into a sphere. The spermatoplasm in the antheridia has meanwhile broken up into a large number of oblong spermatozoids, with a cilium at each end. After this has happened the free extremity of the antheridium bursts open, and the minute spermatozoids are expelled in a swarm into the surrounding water. Some of them reach a neighbouring oogonium, pass through the opened summit into the interior of the receptacle, and there coalesce with the ooplasm which has contracted into a green sphere. In connection with this phenomenon there is the following very striking circumstance to be noted. Where, as is usually the case, an oogonium and an antheridium are developed in close proximity to one another on the same tube, they seldom open simultaneously, and this circumstance most effectively prevents the fertilization of the ooplast by spermatoplasm of the adjacent antheridium; but on the other hand it usually happens that the spermatoplasm from the antheridium of one tube reaches the oogonium of another tube, and in this manner a crossing of the two takes place (figs. 204 [5] and 204 [6]).

As soon as an ooplast is fertilized it surrounds itself with a tough cell-membrane; the green colour of the protoplasm changes to a dirty red or brown, and the fruit is to be seen imbedded in the oogonium in the shape of a reddish-brown, unicellular sphere. The oogonium dissolves or else breaks off with the fruit inclosed in it. In either case the product of fertilization is removed from the tube whereon it developed and sinks to the bottom, where it undergoes a comparatively long period of rest often lasting through an entire winter. When the unicellular fruit germinates, the outer layer of the cell-membrane splits, and out of the rent emerges a tube of like form to that which produced the fruit.

In every case of cryptogamic fertilization hitherto discussed a union of the spermatoplasm with the ooplasm occurs. The protoplasts set aside for the purpose of coalescence forsake the cell-interiors when they have attained to maturity, or at least one of the sexual cells liberates its protoplasm so that it reaches the other unfettered and is enabled to effect a union of their two masses. For this result it is necessary for a part of the cell-membrane enveloping the protoplasm in question to be previously removed, for otherwise it would not be possible to effect the kind of union to which the phrase coalescence of protoplasm is properly applicable. On the other hand, many cases exist in which there is no obvious perforation of the wall, although the changes usually following true fertilization take place. Under these circumstances it is difficult to resist the view that if fertilization (*i.e.* a fusion of protoplasts) really happens (as to which difference of opinion still prevails) it is accomplished by means of osmosis. With this qualification we may say that fertilization by means of osmosis is observed in its simplest form in the Erysipheæ, popularly known as Mildews, in the Moulds allied to *Aspergillus* and *Penicillium,* a description of which in relation to their methods of spore-formation is given on pp. 21, 22, and in several Discomycetes, including the curious Fungus named *Ascobolus,* which will be dealt with more thoroughly when we come to the subject of the mechanisms for dispersing spores.

The Mildew occurring on the surfaces of green foliage-leaves appears under the microscope as a peculiar kind of mycelium. The hyphæ, which are filiform, colourless, and densely interwoven, do not penetrate into the intercellular spaces of the tissue of the host-plant, but satisfy themselves with sinking little suckers into the superficial cells of the leaves and stem (see vol. i. p. 165, fig. 32 [2]). Here and there these hyphal tubes rise erect from the substratum and abstrict moniliform rows of spores; others put forth short, lateral outgrowths which become partitioned off by the insertion of a transverse wall in each, so that the protoplasm in the outgrowth is shut off from the rest of the protoplasm in the tube. Some of these latter structures are oval or club-shaped, and they contain ooplasm and are to be considered as oogonia; the others are cylindrical and sometimes bent into the form of hooks, and they contain the spermatoplasm and constitute antheridia. In a few species the upper, somewhat swollen end of the outgrowth filled with spermatoplasm—*i.e.* the antheridium—bends over the top of the oogonium and attaches itself closely thereto, without, however, sending any special fertilization-tube into the interior of the oogonium; in other Fungi of the Mildew family both cells—the oogonium as well as the antheridium—are spiral and are coiled round one another, and at the same time pressed tightly together. On the assumption that a true fertilization now occurs, this must, as already indicated, be by a diffusion of the spermatoplasm through the cell-membranes to the ooplasm, causing a change in its ultimate structure which corresponds to fertilization. The ooplasm is thereupon converted into an embryo. The cell inclosing the embryo neither dissolves nor severs itself from the parent-hypha, but divides and becomes differentiated into an upper swollen cell and a lower short, stalk-like cell, and below the stalk fresh tubular outgrowths develop from the hyphal filament in question which become septate and ultimately form a voluminous multicellular envelope round the embryo.

The now mature fruit preserves its connection with the parent-hypha, and is to be seen seated upon it in the form of a minute sphere. When a large number of fruits are developed simultaneously on the hyphal reticulum—as is the case in *Sphærotheca Castagnei*, which is parasitic on the leaves of Hops—the grey mildew spread over the foliage has the appearance of being studded with the tiny globular heads. From the embryo a new generation is produced. In the species of the genus *Podosphæra* it develops, within the cellular mass just referred to as investing the fruit, into a single tube (*ascus*). The protoplasm within the ascus breaks up and fashions itself into true spores, which abandon the tube and are distributed by the wind. In *Erysiphe*, on the other hand, the embryo becomes septate, and takes the form of a simple or branched chain of cells, and it is not till after this stage that tubes are produced whose protoplasm is transformed into a group of spores. The tubes in question are long, erect, and club-shaped, and they spring from the cells of the aforesaid chain.

The manner of fertilization and fruit-formation in *Penicillium*, and generally in all the forms of Mould which are comprised under the name Aspergilleæ, is the same as that described in the case of Mildews (Erysipheæ). In them also the extremities of tubular hyphæ which contain the ooplasm and spermatoplasm, respectively, come into close contact. They are either spirally twisted and wound round one another, or else the extremity corresponding to an antheridium is hooked and grasps the other, as is shown in fig. 193[6] (p. 18). Fertilization takes place by osmosis. The embryo produced by the spiral oogonium is septate and multicellular, and develops club-shaped or egg-shaped outgrowths, whose protoplasm breaks up into round or ellipsoidal balls (fig. 193[7]). This structure becomes surrounded by a continuous multicellular tissue, which owes its origin to the upgrowth of a number of hyphæ from the cells at the base of the oogonium. These hyphæ elongate rapidly, ramify, become intertwined, and develop septa until they constitute a spherical envelope round the embryo. The fruit thus constructed is in *Penicillium* about half a millimetre in diameter.

The Florideæ, or Red Seaweeds, are likewise fertilized by means of osmosis. The details of the process are, however, intrinsically different from those observed in Mildews and in the Moulds classed as Aspergilleæ. The organs developed for the purpose of fertilization have also quite a different form in Florideæ. Their most striking feature is the so-called "trichogyne", a long filamentous cell which projects far above the fruit-rudiment. From this structure the characteristic mode of fertilization in Florideæ is called fertilization by aid of a trichogyne. In some Florideæ the cell containing the ooplasm leads directly into the trichogyne; in others the fruit-rudiment which incloses the ooplasm is septate, that is to say, it consists of a row of broad cells which together form a short branch of the ramifying thallus, and adnate to one side of this row of cells is the long, delicate, filamentous cell called the trichogyne (fig. 204[7]). Rudimentary fruits of this kind are produced on one individual, whilst antheridia are formed upon another. It is much less common for fruit-rudiments and antheridia to be developed on the same individual, and in the few species which do exhibit this combination, self-fertilization is rendered practically impossible by a retardation of the development either of the fruit-rudiments or of the antheridia. The antheridium always takes the form of a limited portion of the thallus, from which separate round cells filled with spermatoplasm are thrown off. Fig. 204[8] represents an antheridial branch of *Dudresnaya coccinea.* A slender branch of the thallus terminates in a group of cells arranged dichotomously, and the outermost of these cells, which become rounded off and detached, contain the spermatoplasm, and must be looked upon as spermatozoids. Unlike the spermatozoids of *Vaucheria* and those of the Characeæ (Stoneworts), Muscineæ, and Ferns, to be described presently, these have no cilia, and do not move by virtue of any power of their own in the surrounding water, but are carried about by currents which are always more or less prevalent at the places where the Florideæ live. Through the action of these currents in the sea, the spermatozoids (or *spermatia* as they are called) reach one of the trichogynes and adhere to it, as is shown in fig. 204[7]. The question as to how far attractive forces emanating from the ooplasm come into play in order to effect this conjunction must remain undecided. It is not impossible that substances may be secreted by the ooplasm and be given off into the environing water, and that they may take part in the phenomenon. Nothing more definite is known beyond the evident fact that the spermatozoids adhere much more commonly to trichogynes than to other objects floating in the neighbourhood. Part of the protoplasm of the adherent cells passes apparently by osmosis into the protoplasm of the trichogyne. The change ensuing upon this process is transmitted to the protoplasm occupying the ventral enlargement at the base of the trichogyne, and in many cases even further to the protoplasm of adjacent cells. Although this propagation of the change in the molecular structure of the protoplasm cannot be directly observed, it may be assumed on various grounds, and we may fairly suppose that the action of the absorbed constituents of the spermatoplasm upon the ooplasm is comparable to that of certain enzymes, which have a convulsive effect upon any protoplasm in their vicinity, and even when they are separated from it by cell-walls cause a displacement and rearrangement of the molecules (see vol. i. p. 464). That the change affecting the protoplasm at a particular spot in the fruit-rudiment is capable of being propagated so long as any protoplasm susceptible of the same change is present, is proved by the fact that it is not the trichogyne itself but the ventral enlargement at its base and the cells adjacent to this enlarged portion which undergo subsequent development. They increase in bulk, whereas the trichogyne shrivels and dies. The cells which contain the protoplasm fertilized through the intervention of the trichogyne must, in my opinion, be looked upon as the fruit. Any subsequent structure arising from them is no longer fruit but a new generation. In Florideæ, as in so many other cases, this new generation preserves its connection with the mother-plant, but differs conspicuously in form from the generation from which it sprang. This stage having already been dealt with on p. 22, it is here only necessary to mention briefly that the cells of the fruit begin to shoot out after a period of rest of variable duration and abstrict a mass of spores, and that in addition, in most Florideæ, linear series of cells grow from the cells at the base of the fruit, and form a capsular envelope around the young spores.

The Cryptogams that we have still to deal with, viz.: the Characeæ, Muscineæ, and Vascular Cryptogams, differ from those already described in that the oogonium is wrapped up in a special sheath before fertilization takes place, and that the entrance-passage provided for the spermatoplasm is consequently modified in a characteristic manner. This sheath, to which we shall apply the term *amphigonium* (also known as *archegonium*), is in the main of the same construction in all the plants exhibiting it; but as regards the penetration of the spermatozoids into the amphigonium, and the behaviour of the fruit produced from the fruit-rudiment, there are very considerable differences amongst the groups in question. To follow out these diversities in minute detail is not possible within the narrow limits of this book, and I must content myself in the following pages with giving a brief sketch of the most important phenomena.

To begin with the Stoneworts (Characeæ), we find that in them the fruit-rudiment is ellipsoidal in shape, and is borne on a very short unicellular stalk. This stalk is seated upon the so-called "nodal cell", a short discoid cell which forms the pedestal of the large ellipsoidal oogonium, and also gives rise to five tubular cells arranged in a whorl, and twisted spirally round the oogonium, thus enveloping it in a sheath of great beauty (see fig. 206 [8]). From the ends of these investing tubes, which project above the oogonium, small cells are separated off, and together constitute a little roof for crown to the amphigonium. Beneath the crown the enveloping tubes are drawn together so as to form a neck which incloses a narrow cavity, and this is the part where at the time of fertilization fissures are formed between the otherwise connate tubes of the envelope, thus enabling the spermatozoids to penetrate into the interior of the amphigonium, and to reach the ellipsoidal oogonium there matured.

The mode of genesis of these spermatozoids is extremely remarkable. They are produced in certain red, globular structures, which are slightly smaller than the fruit-rudiments and have a like origin—that is to say, they take their rise amongst the whorls of lateral offshoots. In some species they are formed on the same individuals as the fruit-rudiments (*cf.* figs. 206 [2] and 206 [3]), in others the two kinds of structure develop on different individuals, and are thus separated from one another; hence we distinguish Characeæ into monœcious and diœcious species. Each red sphere is composed of eight plates, outwardly slightly convex. Each of these is in the shape of a spherical triangle with indented edges and folds running radially from the centre to the notched margins (see fig. 206 [4]). The plates are joined together into a sphere, the notches of the margins fitting into one another so as to form a regular dovetailed suture. From the centre of the gently concave inner face of each plate a cylindrical or conical cell projects, carrying upon its summit another, capitate, cell. Each of these head-cells is surmounted by long strings of cells, of which the lowest segments are spherical or cylindrical, whilst the rest are short discs (see fig. 206^{5}). The whole structure may be likened to a whip with many thongs, and the stalk-cell projecting from the plate has hence been called the "manubrium" or handle. So long as the eight plates of the sphere are closed, these manubria project towards the centre of the hollow sphere, and the rows of cells proceeding from the manubria are conglomerated into a ball. But as soon as the plates separate and the sphere falls to pieces, the ball is untwisted and its parts assume the appearance shown in fig. 206^{5}. By this time a spiral spermatozoid has developed from the protoplasm in each of the discoid segments of the filaments, and may be seen lying within its cell (see fig. 206^{6}). But almost immediately afterwards these cells open, and the spermatozoids, which are provided at one end with a pair of long cilia, escape and whirl about in the surrounding

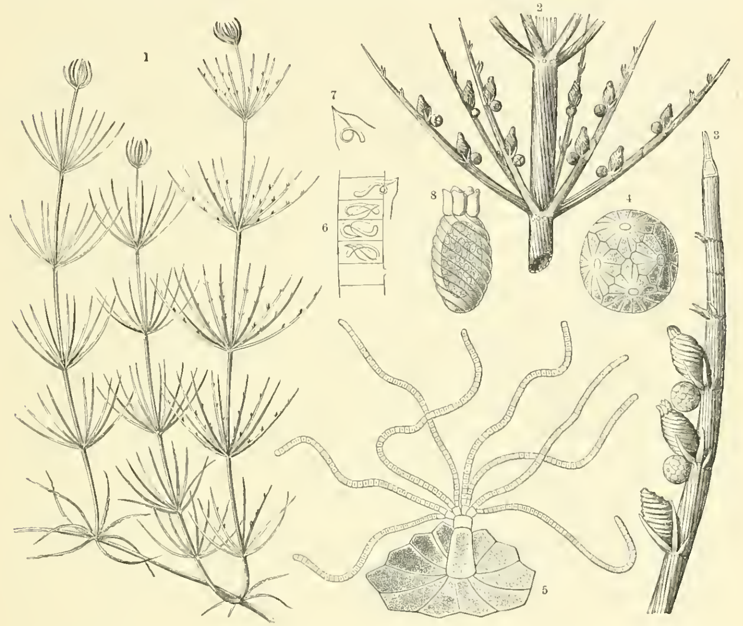

Fig. 206.– Fruit-formation in Stoneworts (Characeæ).

^{1} *Chara fragilis.* ^{2} Piece of the same with amphigonia and antheridia on the branches. ^{3} A single branch with amphigonia and antheridia. ^{4} An antheridium. ^{5} A plate of the antheridium with manubrium and cells grouped in the form of thongs and containing spermatozoids. ^{6} Several cells from one of the whip-like filaments; the cells in the middle contain each a spermatozoid, the spermatozoid is escaping from the uppermost cell, the lowest cell is already vacated. ^{7} A single spermatozoid. ^{8} Amphigonium inclosing the oogonium. ^{1} natural size; $^{2}\times 10$; $^{3}\times 15$; $^{4}\times 35$; $^{5}\times 100$; $^{6}\times 300$; $^{7}\times 500$; $^{8}\times 50$

water (see fig. 206[7]). The spermatozoids then pass through the fissures already described as existing beneath the crown of an amphigonium, and so reach the interior of the latter. Here, in the middle of the cavity is the oogonium (*i.e.* the great cell containing the ooplasm), and over it there is a slimy gelatinous mass, which occupies more particularly the neck of the amphigonium. The cell-membrane of the oogonium is attenuated and almost liquefied, and these soft and swollen masses of mucilage do not interfere in any way with the progressive motion of the spermatozoids. The latter reach the ooplasm, and, so far as we can see, a coalescence of the two kinds of protoplasm takes place.

The changes set up in the fruit-rudiment by fertilization first manifest themselves externally in an alteration in colour. The chlorophyll-bodies, hitherto green, assume a reddish-yellow tint; the spiral cells of the amphigonium become thickened and nearly black, and the amphigonium constitutes a hard shell which acts as an outer envelope inclosing the inner envelope of the fertilized ooplasm, now converted into an embryo. The entire structure next detaches itself from the stalk-cell, sinks under water, and remains for a considerable time—usually through the whole winter — lying unchanged at the bottom of the pond. The embryo does not germinate till the following spring, when it begins by developing a linear series of cells, the so-called pro-embryo, and from one of the cells of this pro-embryo is produced a Stonewort plant with branches in whorls as before (see fig. 206[1]).

The fruit-rudiment in Muscineæ (Mosses and Liverworts) exhibits in many respects a resemblance to that of a Stonewort, although its origin is quite different. It takes its rise from a superficial cell of the Moss-plant, and the cell belongs, according to the species, either to the foliaceous or to the cauline portion of the thallus. This cell projects in the form of a papilla above the adjoining cells, and becomes partitioned by a transverse wall into an under and an upper cell, the former of which serves as a pedestal to the body of tissue developed from the upper cell. The cellular body referred to is differentiated, by repeated insertion of longitudinal and transverse walls, into a central row of cells and an envelope. Amongst the central cells one situated somewhat low down in the series is conspicuous for its size; it contains the ooplasm, and must be looked upon as an oogonium. The central cells, which are placed in succession above it, are called the canal-cells of the neck. The name is derived from the fact that they occupy the constricted portion or neck of the envelope. The cellular envelope, which incloses the central row of cells and constitutes the amphigonium, is shaped like a flask (see fig. 191[10]); the lower, enlarged, ventral portion conceals the oogonium, the upper constricted portion is filled up by the neck-cells, and the whole structure, which received from the earlier botanists the name of "archegonium", is closed at the top by a lid composed of several cells. When the time for fertilization arrives the canal-cells of the neck swell up and are converted into mucilage. The lid-cells open and part of the mucilage is forced out; what remains offers no impediment to the admission of the spermatozoids to the ooplasm in the centre of the fruit-rudiment.

The antheridia arise in the same manner as the fruit-rudiments. A superficial cell of the thallus is enlarged into a papilla, and, by the repeated partition in all directions of its first segments, a body of tissue is produced, which includes a delicate stalk and a thickened upper portion, either clavate or spherical in shape. The latter part consists of a multicellular sac-like envelope and a parenchymatous filling-tissue inclosed within the envelope. In each cell of the internal tissue the protoplasm fashions itself into a spirally-bent spermatozoid, and shortly afterwards the entire filling-in tissue is resolved into its separate cells. The antheridium now opens at the top, and the loose cells with the mucilage in which they are embedded are ejected into the surrounding aqueous medium composed of rain or dew-drops. The spermatozoids then escape from their delicate cell-membranes, and swim about the water by the help of the two long cilia wherewith each is furnished (see vol. i. p. 29, figs. 7^9 and 7^{10}). Passing down the open neck of the amphigonium, now filled with mucilage only, they succeed in reaching the oogonium in the enlarged base of the fruit-rudiment and apply themselves closely to its surface; a constituent portion of the spermatoplasm is absorbed into the ooplasm with the result that the latter becomes fertilized.

Usually several antheridia are situated close together. In Mosses they are mingled with paraphyses, structures resembling hairs, the significance of which has not yet been explained. In many species one individual develops only antheridia, another only amphigonia; but in other species antheridia and amphigonia are developed side by side on the same Moss-plant. Where the latter is the case either the oogonium exhibits an earlier development than the antheridium, or the reverse is the case. Either the passage leading to the oogonium through the neck of the amphigonium is opened whilst the adjacent antheridia are still closed, or else the spermatozoids are set free from the antheridia at a time when access to the oogonium is still barred by the lid-cells of the amphigonium. As in so many cases of a similar kind this contrivance prevents a union between the ooplasm and the spermatoplasm produced by the same individual, and favours cross-fertilization between different individuals.

In some Liverworts the antheridia and amphigonia are surrounded by annular walls, and these organs then appear to be sunk in depressions of the thallus. In other Liverworts separate lobes or branchlets of the thallus are transformed into stalked shields or discs, and the antheridia and amphigonia are formed in special niches and compartments on the surface of the shields. Those Muscineæ which have their thalli differentiated each into a cauline axis and cellular laminæ resembling leaflets, develop antheridia in the axils of the leaflets, or else in pitcher-shaped cavities at the tops of the stems. In Mosses the principal or secondary axes terminate in groups of antheridia or amphigonia, and specialized leaflets act as envelopes or roofs and constitute the "perichætium". Sometimes these leaflets have the appearance of floral leaves, as, for instance, in the Hair-Mosses (*Polytrichum*), one species of which is represented in Plate IX. in the foreground to the left. The antheridia and amphigonia are here distributed on different individuals.

The investing leaflets at the summit of those stems which terminate in antheridia are crowded close together; they are short, broad, and of a brownish-red colour, and look like small floral-leaves seated upon a disc-shaped receptacle. *Polytrichum* is a typical instance of the Mosses which exhibit a conspicuous contrast between the investing scales of antheridia and those of amphigonia. The perichætium in individuals which produce only amphigonia possess an altogether different form and arrangement of parts from the corresponding structure in antheridia-bearing individuals. The difference is shown in Plate IX. The *Polytrichum*-stems, which are seen in the picture standing up behind those terminating in flower-like discs, have no antheridia, but send up slender bristles, on each of which is borne a spore-case. These, however, are the products of amphigonia, which lie concealed amongst the long green leaflets at the tops of the stems, and have there undergone fertilization.

As before said, there is a close resemblance between Muscineæ and Characeæ as regards the position of the ooplasm to be fertilized in the middle of the amphigonium, the genesis and form of the spermatozoids, and, lastly, the process of fertilization. But from the moment of fertilization the course of development is altogether different. The fruits of Characeæ become detached from the mother-plant, whereas those of Muscineæ remain in connection with it, and this connection is not merely mechanical but organic. The generation developed from the Moss-fruit continues to derive the nutritive substances requisite for its growth and completion from the mother-plant, and without the support of the latter it would inevitably perish. The word support may here be used in a wide sense; for the mother-plant is actually the bearer or stay of the new generation, which is produced from the ooplasm converted by fertilization into an embryo, and it may be compared to a tree with Mistletoe growing upon its boughs. In Characeæ the separate stages of development are always quite distinct; the stage of maturity in particular being characterized by the falling away of the fruit from the mother-plant. This is not the case in Muscineæ. Since no separation in space takes place, it is also difficult to establish time-limits and to say when the fruit has attained maturity, and the difficulty is increased by the fact that no sufficient indications are afforded by alterations of shape or colour. It is best to look upon the formation of fruit as being complete as soon as fertilization has taken place; from this moment the ooplasm must be considered to be an embryo, and its envelopes to be fruit-coats. Evidence in favour of this conception of the phenomenon is afforded by the circumstance that after the union of ooplasm and spermatoplasm development is arrested, and a period of repose ensues, whereas both before and afterwards the outward manifestations of change follow one another in rapid succession. A description of the subsequent changes has been already given (see pp. 15, 16), and we need only repeat here that the generation which springs from the Moss-fruit develops spores and, after having scattered them abroad, dies away.

The strongest likeness exists between the fruit-rudiments and antheridia of Muscineæ and those exhibited by Ferns, Horse-tails, Rhizocarps, and Club-Mosses,

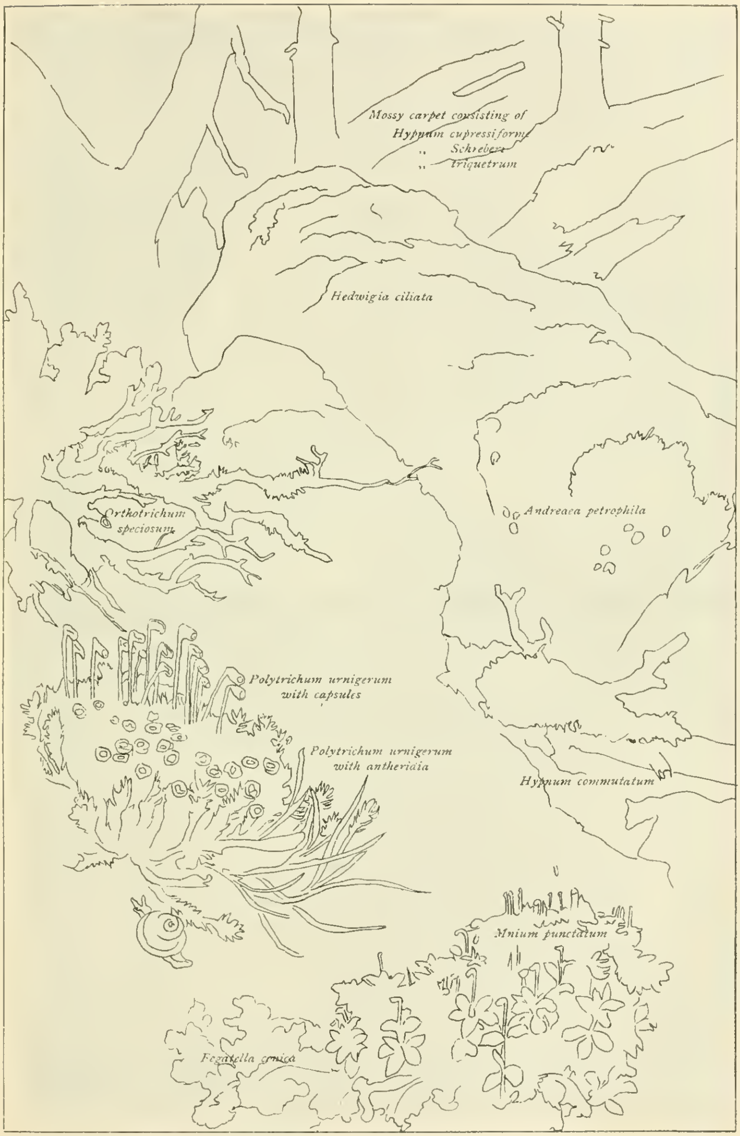

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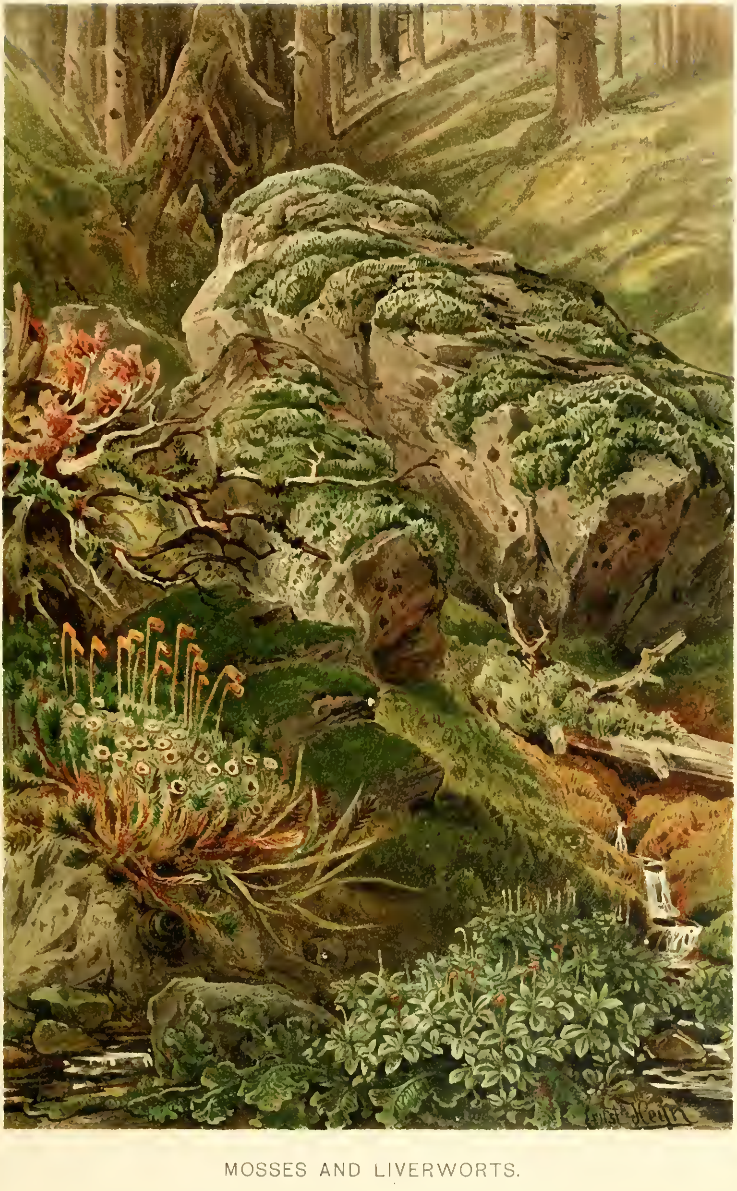
PLATE IX.



MOSSES AND LIVERWORTS.

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all of which are classed together under the name of Vascular Cryptogams, on account of the presence of vascular bundles in their stem-structures and phylloclades. The first generation of these Vascular Cryptogams, whereon are developed the antheridia and fruit-rudiments, also resembles in an unmistakable manner the first generation in certain Liverworts.

In Ferns, which constitute the most extensive section of the Vascular Cryptogams, and may be taken as their type, the first generation makes its appearance in the form of a flat, green, foliaceous structure, usually reniform or heart-shaped, lying in close contact with the nutrient soil (see fig. 189^{16}). Inasmuch as the tissue of this first generation nowhere contains vascular bundles, it must be looked upon as a thallus, and has received the name of *prothallium.* The Fern-prothallium bears the fruit-rudiments as well as the antheridia upon its under surface, which is in contact with the nutrient soil, and which adheres to it by means of a number of delicate hair-like suction-cells. Some Ferns develop the fruit-rudiments and antheridia on separate prothallia; others produce them both on the same prothallium. In the latter case the fruit-rudiments are situated near the sinus of the prothallium, and the antheridia on the part remote from the sinus. Each fruit-rudiment may be compared to a flask in shape, and arises from a superficial cell of the prothallium which is only slightly arched outwards. This cell is divided by the insertion of two partition-walls into three cells, each of which is again segmented in definite directions. From the uppermost cell is produced a tissue which forms the neck of the flask-shaped fruit-rudiment; the middle cell gives rise to three cells, of which the two upper, the canal-cells, occupy the neck, whilst the undermost one becomes the relatively large and subsequently rounded ooplast. The daughter-cells developed from the lowest primary cell take the form of an investing wall round the ooplast, or, to return to the analogy of a flask, constitute the wall of the ventrally enlarged portion of the flask. The protoplasm of the ooplast is the ooplasm, and is now to be seen surrounded by a pluricellular tissue, which, as in the case of Characeæ and Muscineæ, may be called an amphigonium. Only the neck of the amphigonium projects above the other adjacent tissues of the prothallium; the enlarged ventral portion is, as it were, sunk in the substance of the prothallium.

The antheridia are also developed from cells upon the surface of the prothallium. These cells project in the form of papillæ above the surrounding tissue and undergo division by the introduction of partition-walls. The outermost daughter-cell becomes enlarged and assumes a globular shape, and from the protoplasm in its interior are formed spiral spermatozoids. Another mode of origin consists in the formation of a papilliform or hemispherical protuberance of tissue which shows unmistakably a differentiation into central cells destitute of chlorophyll and enveloping cells containing chlorophyll. The former divide up and a filling-in tissue is formed, the small constituent cells of which contain spermatoplasm. After the development of a spermatozoid in each of these small cells, the whole of the filling-in tissue falls to pieces, that is to say, the individual cells separate from one another and remain for a short time disconnected but still in contact. At length the top of the antheridium opens; the loose cells are discharged into the surrounding water derived from rain or dew, and from each of them is set free a spirally-coiled spermatozoid furnished as regards its anterior half with bristling cilia (see vol. i. p. 29, fig. 7[11]). The spermatozoids manifestly direct their course to an amphigonium as they whirl about in the water. Meanwhile the canal-cells of neck of the amphigonium have been partially converted into mucilage; some mucilage is discharged into the environing water, and it seems that concomitantly with this organic acids have been evolved in the region of the amphigonium, which exercise an attractive influence on the spermatozoids. What is known as a fact is that the spermatozoids accumulate in this mucilaginous mass and also penetrate through the slimy substance left behind in the canal of the amphigonial neck. Thus they reach the ooplasm which is hidden in the oogonium at the bottom of the fruit-rudiment. As it has repeatedly been observed that spermatozoids make their way into the ooplasm and there disappear, we may assume that the delicate envelope of the ooplast is pierced by the spermatozoid, and that thereupon a coalescence between the two kinds of protoplasm takes place (*cf.* also figs. 346[1, 2, 3, 4]).

The fertilized ooplasm now subdivides into several cells with partition-walls inserted between them, and thus is produced a multicellular embryo which remains embedded in the unaltered amphigonium. This structure, though scarcely differing at all from the fruit-rudiment, must be considered as a fruit. After a short period of rest the embryo germinates, and the new generation, which gradually makes its appearance as stem, roots, and fronds emerging from the embryo, continues for a short time to receive its food-stuffs through the mediation of the parental prothallium. At length, when the new generation has grown sufficiently strong, and is capable of taking up food-stuffs directly from the surrounding air and soil, and of transforming them into constructive materials, the assistance of the prothallium becomes superfluous. The prothallium then withers, and by the time the sporogenous fronds have developed it has vanished, and no trace of it remains.

The Horse-tails (Equisetaceæ) have, in the main, the same features as the Ferns just described as typical of the Vascular Cryptogams in all that relates to the forms of prothallium, antheridia, and fruit-rudiments. The prothallium produced from the spore is at first delicate and ribbon-shaped, but later becomes multifariously lobed, and in form recalls the thallus of certain Liverworts, or sometimes even resembles a little curled foliage-leaf. In most species antheridia and fruit-rudiments grow on different prothallia. Where this is not the case, fertilization of the ooplasm by spermatoplasm arising from the same individual is rendered impossible by means of a disparity between the organs concerned in respect of the time at which they mature. The prothallia which give rise to antheridia are always much smaller than those which produce the fruit-rudiments. The antheridia develop from superficial cells at the end or on the margin of the lobate prothallium, whilst the fruit-rudiments, on the other hand, are derived from superficial cells in the recesses between the lobes (see fig. 190[8]). The spermatozoids have a spatulate enlargement at one extremity, and carry on the other, attenuated end a regular mane of extremely fine cilia.

Far more important are the characteristics which distinguish from Ferns the Rhizocarpeæ and Lycopodiales, especially the genera *Salvinia, Marsilia,* and *Selaginella,* in all of which the development has been studied with great care. The antheridia-bearing prothallia are, in the last-mentioned genera, extremely different in point of size from those which bear fruit-rudiments. Both prothallia, it is true, have spores for their starting-points, but these spores themselves have different dimensions, and are distinguished as *microspores* and *macrospores* (*i.e.* small spores and large spores). The microspores are the parts of the plant where antheridia are formed, and the macrospores those where fruit-rudiments are formed. In a microspore the protoplasm divides into several parts, and partition-walls are inserted between them, thus forming a tissue composed of a very few cells, the greater part of which remains concealed in the interior of the spore. Only one or two superficial cells of this tissue push out through rents made here and there in the coat of the spore, and these protruded cells constitute the antheridia. The apical cell of the antheridium becomes filled with a tissue, and in each cell of this tissue is formed a spirally-coiled spermatozoid. The opening of the antheridium and the escape of the spermatozoids then ensues in the same manner as in Ferns. The prothallium which originates from a macrospore and is the seat of formation of fruit-rudiments, although it is larger and composed of more cells than that just described, does not forsake the interior of the cavity of the macrospore to any greater extent, but only protrudes a little at one place where the tough outer coat of the macrospore is ruptured. Two kinds of tissue are in reality developed within the limits of each macrospore, viz.: the one above referred to as emerging between the torn edges of the outer spore-coat, and a tissue of reserve material deposited at the bottom of the macrospore. The latter is very rich in starch and oil, and serves as a storehouse of nutriment for the prothallium at least until it is in a position to get food for itself out of the environment. The fruit-rudiments (amphigonia) appear on the protruding portion of the prothallium, and are entirely buried in its tissue. The development of the fruit-rudiment, the formation of canal-cells which subsequently turn into mucilage, the penetration of the spermatozoids, and the act of fertilization, are in all essential respects the same as the corresponding processes in Ferns, and therefore a description of them in detail may here be dispensed with.

The tissue produced from a macrospore in the Rhizocarpeæ and Selaginelleæ has been compared to the ovule as it occurs in the Phanerogams which will be the subject of the next chapter, and certain actual analogies have been brought out which are exhibited by the ooplasm when converted into an embryo, the store-chamber for food-stuffs, and the protective envelope in each case. Having regard to the identity of object aimed at through the instrumentality of these structures in the most widely different sections of the Vegetable Kingdom, such analogies are really a matter of course, and if naturalists limit themselves to proving that organs which have the same functions, however greatly they may differ in form, yet always possess certain similarity, and that this similarity increases in a conspicuous degree when the external conditions of life are the same, no objection can be made to the generalization. But if it is made the basis of far-reaching speculations and of hypotheses concerning the evolution of one group of plants from another, the descent of Phanerogams from Cryptogams, for example, I must enter an emphatic protest against any such proceeding.

THE COMMENCEMENT OF THE PHANEROGAMIC FRUIT.

Long experience has shown us that the propagation of plants is accomplished with much greater certainty by means of Brood-bodies than by Fertilization and production of Fruit. For a fruit to be formed, two portions of protoplasm which have arisen separately must be brought together. Such a union denotes that at least one of the two protoplasts in question is endowed with a capacity for translation, that the male cell is not obstructed on its way to the female, and that facilities are present to promote its union with that cell. But there's many a slip 'twixt the cup and the lip! Adverse winds, unfavourable currents, long-continued drought, uninterrupted rain, these and many another unexpected circumstance may bar the way to fertilization. Often enough fertilization is hindered from causes such as these, and in consequence the young fruit-rudiment atrophies, the embryo is not formed, and the plant, in order to propagate, must rely on its brood-bodies.

That fruits do not miscarry oftener than they actually do is due to the fact that the difficulties of the situation from external cause, are to some extent met by the position of the egg-cell and the form of the young fruit. In other words, the fashioning of the organs concerned in the production of fruit is adapted to the circumstances of the environment.

Perhaps the obstacles are at a minimum in the case of plants in which fertilization is accomplished under water. The cells in question here require no especial protection. The surrounding water maintains them in the proper position, brings food to them, and protects them from drying up. In it they both live and move. Thus it is intelligible why so many plants which live under water, or which use water for the accomplishing of fertilization, are destitute of any but the simplest envelopes for their spermatoplasm and ooplasm. Complicated investments are valueless under such circumstances, possibly even disadvantageous; in any case they are superfluous. Nor is it usual in plants to produce superfluous structures. As we know, aquatic plants do not possess woody stems and branches. And for this reason. Tissues of this kind are not required, since the surrounding water buoys them up in the proper position so that hard wood and bast are not needed. So also with the ooplasm and spermatoplasm. Cryptogamic plants which fruit under water do not possess complex ovaries like Phanerogams, as they are unnecessary. Just before the time of fertilization the spermatoplasm is segmented up into many fragments; these escape from the antheridium and reach the simple fruit-rudiment by swimming. Since the spermatozoids are attracted to the young fruits by certain excretions which the latter pass out into the water, the multifarious devices associated with aërial fertilization are unnecessary. Protective coats around the sexual organs, sheaths to limit evaporation, brightly-coloured or sweet-smelling floral-leaves to attract insects that they may transfer the pollen from flower to flower—all these are wanting in plants which are fertilized under water. Now it is just these accessory protecting structures which constitute what are called blossoms. Thus we can say that these water-plants have no blossoms. To avoid misconception it must be stated that although they have no blossoms they have flowers. For although, popularly, blossoms and flowers are used as synonymous terms, under flowers are comprehended the organs which are concerned in fertilization, under blossom merely the leaves which inclose the essential organs and which guard and protect the young fruits and stamens. It is these latter which produce the sexual protoplasts. Their union is promoted by the leaves of the blossom. Sometimes they catch the pollen-grains as they are blown by the wind, or by the production of honey and scents attract insects which remove the pollen in their visits. In other cases, by projecting ridges and corners, they are instrumental in detaching the pollen from these same insects, and in a thousand ways protect and assist the difficult process of aërial fertilization.

In the above lines we have been speaking not of aquatic plants generally, but of such as are fertilized under water. And these should be carefully distinguished. Many aquatics, which pass their lives under water, send up their flowers to the surface so that their fertilization is aërial. On the other hand, strange though it may seem, the fertilization of most aërial Lichens, Mosses, and Ferns which grow on the sand of desolate moors, on the sunny rocks of mountain sides, or on the dry bark of old tree stems, is accomplished under water. Plants of this sort may be exposed to drought for many months, and the movement of sap within them may be suspended; but when they are moistened with rain or dew they are quickened and rejuvenated, and form their young fruits and antheridia. Things are so arranged that the liberation of the spermatozoids coincides with the moment at which these plants have access to sufficient moisture. Thus we see that it is literally true of these plants—whether growing on the bough of a tree or in a ravine on a mountain side—that their fertilization is accomplished under water.

The only really important distinction between plants permanently submerged and such as are thus situated from time to time, is that in the latter the young sexual organs are protected against desiccation during the periods of exposure by means of sheathing structures and leaf-like scales, as is particularly well shown by the Mosses. Blossoms in the usual sense, however, are not found amongst Ferns and Mosses, and we can make the following three general statements:—(1) That Cryptogams are fertilized under water and most Phanerogams in the air; (2) that

Cryptogams lack blossoms, since these are not necessary for aquatic fertilization; (3) that almost all Phanerogams, on the other hand, possess blossoms, since they are required to protect and promote aërial fertilization.

The very complicated structure of the parts immediately adjacent to the region where the sexual protoplasts are developed depends upon the fact that fertilization is aërial. The portions of protoplasm destined for fertilization can only be adequately elaborated if their enveloping membranes are thin and delicate, and suited for the osmotic transfer of materials. Such a membrane, however, is incapable of protecting the protoplasm from the drying influence of the air; it is absolutely essential that both the spermatoplasm and the ooplasm shall be protected during the critical period by a suitable envelope. Thus one finds in all Phanerogams—quite apart from the perianth—a protective mantle developed around the sexual cells. This mantle has its cell-walls suitably thickened; its outer layers afford the necessary resistance to desiccation, whilst deeper down an ample supply of water is maintained.

These characters are well shown in that constituent of the ovary from which the seed will be ultimately produced. This portion is known as the *ovule.* Every ovule consists of a mass of tissue, the *nucellus* of the ovule in which the ooplasm or egg-cell is concealed, and an enveloping sheath, the *integument,* which may be either single or double. Such ovules are borne in the genus *Cycas* (figs. 208 [7] and 208 [8]) without further covering than a fretwork of hairs which protects them against too great drying up. In other Cycads and in the majority of Gymnosperms, of which the Cypress and Juniper, the Pine and the Fir, may be quoted as examples, the leaf-like scales of the young fruit are so arranged that the ovules produced on their surfaces are hidden from view and secure against outside danger. In the other Phanerogams (the Angiosperms) the ovules are concealed in a closed chamber—the pistil—the lower enlarged portion of which is known as the *ovary.*

In the construction of this chamber the chief part is taken by the floral axis and by the floral-leaves known as *carpels.* So unequal, however, is the share taken by these parts in the structure of the ovary that in some cases it is formed almost entirely from the floral axis, and in others almost entirely from the carpels. In consequence the apex of the floral axis, which is known as the floral *receptacle,* shows an extraordinary variety of form. Thus in one series of plants the receptacle is not excavated, but solid, assuming the form of a knob, hemisphere, or cone (figs. 207 [8] and 207 [9]); whilst in others it is concave and excavated (figs. 208 [1] and 208 [2]). The forms met with in nature can be produced artificially by taking a conical mass of soft wax and flattening its summit, then gradually pressing it down into a saucer-like shape, and so on until one has produced a hollow bowl. So in nature we have at one extreme the solid cone, at the other the hollow vessel. Between these two extremes, between the conical and excavated receptacles, we have the flat or disc-like receptacle. It is hardly necessary to point out that in the growth and differentiation of the living plant the excavated receptacle is not the result of any actual hollowing-out process as in the lump of wax, but is due to unequal growth of the different parts of the receptacle—the peripheral parts growing up as a circular wall around the central parts, so that the form of a cup or urn is gradually assumed. When one speaks of the excavation of the receptacle one is speaking figuratively—there is no excavation in a literal sense.

The configuration of the receptacle is further complicated by the fact that the centre of the receptacle does not always cease growing, but grows up as a cushion or peg; thus we have a receptacle having the form of a conical peg with a peripheral, urn-like wall around it.

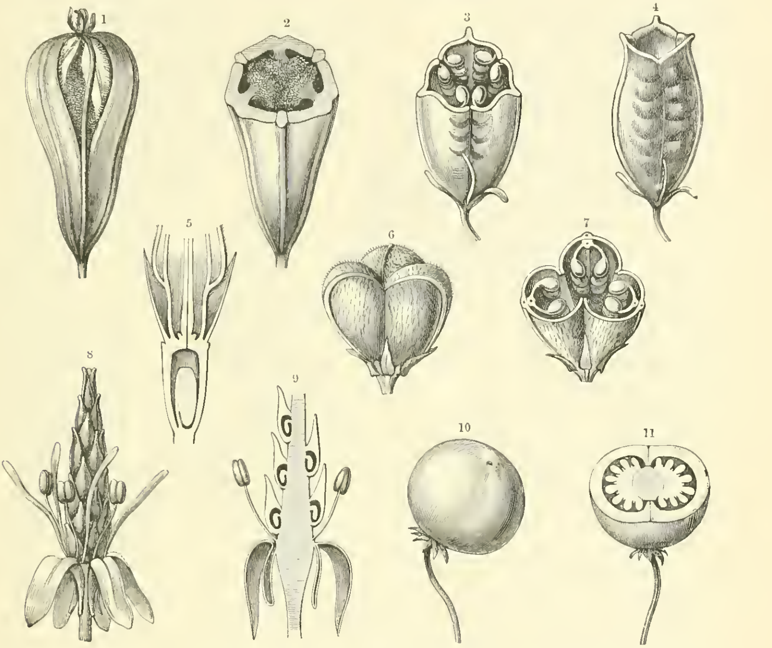


Fig. 207.—Structure of Phanerogamic Ovaries.

[1] Dehisced fruit of *Miltonia stellata*. [2] Ovary of *Miltonia* cut across transversely. [3] Ovary of Mignonette (*Reseda*) cut across transversely. [4] The same ovary intact. [5] Longitudinal section of the ovary of the Jerusalem Artichoke (*Helianthus tuberosus*). [6] Ovary of the Violet (*Viola odorata*). [7] The same, cut across. [8] Receptacle and carpels of *Myosurus minimus*. [9] The same in longitudinal section. [10] Young fruit of Potato (*Solanum tuberosum*). [11] The same cut transversely. All the figures considerably magnified.

In describing the relations of the floral-leaves to the receptacle it will be simplest to commence with the conical receptacle. Here the floral-leaves are found arranged in whorls above one another or in a continuous spiral. At the top are the carpels, below these the stamens, and below these again the leaves of the perianth. Of these various kinds of leaves there may be developed one, two, or even more whorls. When several whorled carpels are united together so as to inclose a single chamber, the tip of the receptacle may be produced above the point of insertion of the carpels and project into the ovarian cavity, or it may penetrate the ovary as a central column. On the other hand, each carpel may give rise to a separate chamber, in which case one finds a whorl of distinct ovaries at the tip of the receptacle (fig. 210^{7}); or there may be numerous small ovaries spirally arranged around the receptacle (figs. 207^{8} and 207^{9}).

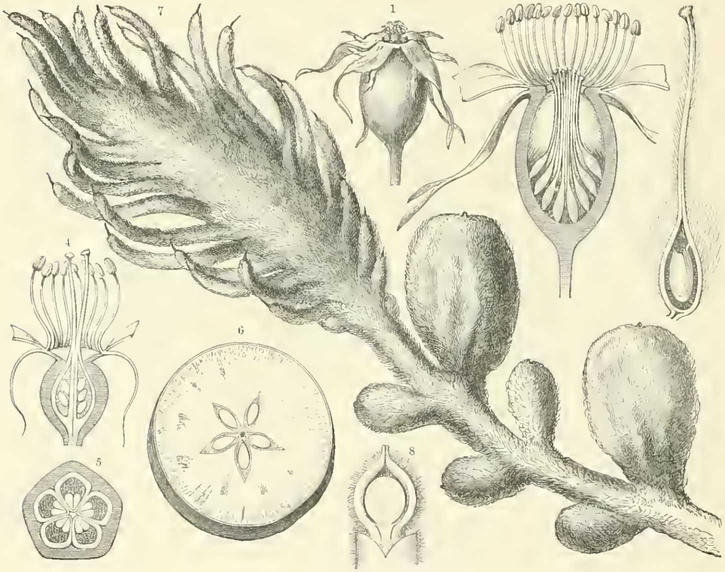


Fig. 208.—Structure of Phanerogamic Ovaries.

^{1} Excavated receptacle and carpels of a Rose (*Rosa Schottiana*). ^{2} The same in longitudinal section. ^{3} A single carpel of the same in longitudinal section ^{4} Ovary of the Apple (*Pyrus Malus*) in longitudinal section. ^{5} The same in transverse section. ^{6} Transverse section of a ripe Apple. ^{7} Carpel of *Cycas revoluta* with ovules. ^{8} Longitudinal section of an ovule of *Cycas*. ^{1}, ^{6}, ^{7}, ^{8} natural size; ^{2}, ^{4}, ^{5}×3; ^{3}×8.

In order that the position and mutual relations of the various floral-leaves on disc-like and excavated receptacles may be intelligible it is necessary that we should return to the lump of wax. Let the cone of wax be pressed down so that it assumes the form of a disc or cup. Assuming the floral-leaves to be present upon it during this process—covering the cone from base to apex—when the disc stage is reached the leaves formerly present at the apex will occupy the centre, those at the base the periphery of the disc. If the wax be further moulded into a cup the leaves previously at or near the apex of the cone will occupy positions within the cup—those immediately at the apex being at the centre—whilst those near the base will be found on the edge of the cup.

According as the leaves are inserted spirally or in whorls upon the receptacle, whether they are present in single or double cycles, whether they are fused with one another or with the receptacle—all these offer almost infinite possibility of variation in form, so manifold, indeed, that their complete description is quite beyond the limits of the present work. Here the forms described must be limited to a series of more or less typical cases; they are for the most part selected from well-known and widely-distributed plants readily accessible to any one.

To avoid repetition the seventeen selected cases are arranged in two groups, of which the first group includes forms with a conical receptacle, the second such as have a disc-like or excavated receptacle. Each of these groups is further subdivided, according as the carpels are all of one sort or of two sorts.

OVARIES ON A CONICAL RECEPTACLE.

Carpels all of One Sort.

(1) The carpels are inserted spirally on the receptacle. Each carpel contains one or several ovules. The receptacle is either much elongated, as in the Mousetail (*Myosurus*, figs. 207 ^{8} and 207 ^{9}), or conical, as in the Tulip-tree (*Liriodendron*), or button-like, as in the Crowfoot (*Ranunculus*).

(2) The carpels are inserted in whorls upon the receptacle, their margins are infolded and fused with the prolonged apex of the receptacle. Since they are also fused with one another below, they collectively form a multilocular ovary. Each carpel bears ovules over its inner surface. As examples may be quoted the Yellow Water-Lily (*Nuphar*), and the Flowering Rush (*Butomus*, figs. 210 ^{7} and 210 ^{8}).

(3) The carpels are inserted in a whorl at the summit of the receptacle and are fused with one another. The receptacle does not project into the ovarian cavity. Each carpel bears ovules either along its margins, as in Mignonette (*Reseda*, figs. 207 ^{3} and 207 ^{4}), or on its internal surface, as in the Sundew (*Drosera*), or basally, as in *Dionæa*, *Drosophyllum*, and in *Caylusea* (Resedaceæ). In *Reseda* the ovary is open above.

Carpels of Two Kinds.

(4) The carpels arise at the tip of the receptacle in two alternating whorls of two each. The two upper carpels are reduced to midribs on which the ovules are borne in two rows. A delicate membrane is stretched like a tympanum between these two midribs which form the frame. The two lower carpels are destitute of ovules and are fixed like valves to the upper pair. This form is met with in numerous modifications in the Cruciferæ.

(5) The carpels arise in two whorls at the tip of the receptacle. Those of the lower whorl are destitute of ovules and form the ovary, those of the upper whorl are modified into strings or cushions, and are fused with the inner surface of the

lower carpels. They bear the ovules. Examples:—the Violet (*Viola*, figs. 207 [6] and 207 [7]), the Celandine (*Chelidonium*), and the Poppy (*Papaver*).

(6) The lower whorl of carpels are united edge to edge, inclosing the ovarian cavity. They are destitute of ovules. The tip of the receptacle projects a very short distance into the ovary, and bears a single ovule-bearing carpel which is apparently terminal upon it. Examples:—the Rhubarb (*Rheum*), and Dock (*Rumex*, fig. 212 [23]).

(7) The lower whorl of carpels are united edge to edge like staves, forming the ovary into which the apex of the receptacle projects as a central column. The upper ovuliferous carpels are metamorphosed into cushion-like structures consolidated with the receptacular column. These cushions are either arranged spirally, as in *Glaux* (figs. 211 [8] and 211 [9]), or in a whorl, as in *Primula Japonica.*

(8) The lower carpels are inserted in a whorl, and have their margins infolded, and are fused together so as to form a multilocular ovary. The upper, ovuliferous carpels arise from the tip of the receptacle, which is continued through the centre of the ovary. The ovules project into the cavities of the ovary. Examples:—The Spurge (*Euphorbia*), *Azalea*, Foxglove (*Digitalis*), Potato (*Solanum*, figs. 207 [10] and 207 [11]).

OVARIES ON A FLAT OR EXCAVATED RECEPTACLE.

Carpels of One Sort.

(9) The carpels are arranged spirally upon a raised central cushion of the *flat* receptacle. Each carpel forms a distinct ovary containing one or more ovules. Examples:—*Dryas, Potentilla,* the Raspberry (*Rubus Idæus*, figs. 210 [11] and 210 [12]).

(10) The carpels are arranged spirally within an *excavated* receptacle. Each carpel forms a distinct ovary containing one or more ovules. There is no fusion between the walls of the carpels and that of the receptacle. Example:—The Rose (*Rosa*, figs. 208 [1, 2, 3]).

(11) A single ovuliferous carpel is inserted in the centre of an excavated receptacle. It is apparently terminal upon the axis, and is not fused with the excavated receptacle. This condition prevails in the Cherry, Plum, Apricot, and Almond (*Amygdalus*, figs. 209 [6] and 209 [7]).

(12) The carpels arise in a whorl from the end of the axis at the base of an excavated receptacle. Their margins are infolded, and they are fused together into a multilocular ovary. The ovary fills the whole cavity of the receptacle, with the inner wall of which it is fused. Ovules are borne by the infolded margins of each carpel. Examples:—The Medlar (*Mespilus*), Pears and Apples (*Pyrus*, figs. 208 [4, 5, 6]).

(13) The carpels arise from the tip of the axis at the base of the excavated receptacle. The receptacle has a remarkable structure; it is like a bottle in shape with three portions of the wall removed, so that it is reduced to three ribs which join above and bear the other parts of the flower. The apertures in the receptacle are occupied by the three carpels. Thus the ovary consists of three carpels and

three receptacular ridges. The ovules are borne on longitudinally-running cushions on the carpels. This class of ovary is found in great variety amongst the Orchidaceæ (figs. 207 [1] and 207 [2], and figs. 212 [1, 2, 3, 4]).

Carpels of Two Kinds.

(14) One series of carpels, destitute of ovules, arise from the margin of the deeply-excavated receptacle, roofing it in. Another series, metamorphosed into ovule-bearing strings, arise spirally from the inner wall of the receptacle and project into the ovarian cavity. Examples are afforded by the Cactaceæ, *e.g.* *Opuntia* and *Cereus* (figs. 209 [1] and 209 [2]).

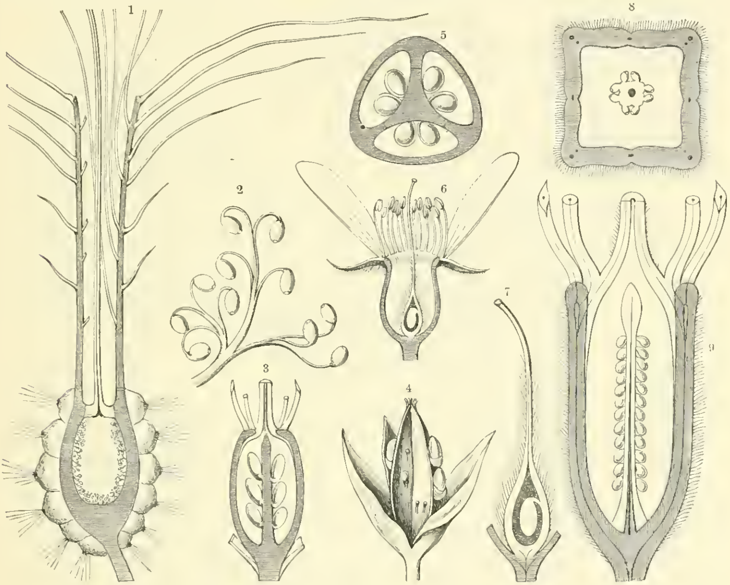


Fig. 209.—Structure of Phanerogamic Ovaries.

[1] Longitudinal section of the ovary of *Cereus grandiflorus.* [2] Ovules on a branched placenta from the base of the ovary of *Cereus.* [3] Longitudinal section of the ovary of *Hedychium angustifolium.* [4] Dehisced fruit of the same plant. [5] Transverse section of the ovary of the same. [6] Longitudinal section of an Almond flower (*Amygdalus communis*). [7] Longitudinal section of the ovary of the same. [8], [9] Transverse and longitudinal sections of the ovary of the Willow-herb (*Epilobium angustifolum*). [1] natural size; [3], [4], [5], [6] slightly magnified; [2], [7], [8], [9] ×10.

(15) One series of carpels closes the mouth of the excavated receptacle, as in (14). The other series, bearing the ovules, are filamentous, and arise as a whorl from the base of the receptacle; they are consolidated with a thread-like prolongation of the tip of the axis which runs up as a central column. Example:—The Willow-herb (*Epilobium*, figs. 209 [8] and 209 [9]).

[These two figures are slightly inaccurate in that the partitions of the ovarian cavity are not indicated. In the cross-section, fig. 209^{8}, they would run diagonally from the corners to the central column. In allied forms they are sometimes incomplete.—*Ed.*]

(16) One series of carpels as in (14) and (15). The other series are metamorphosed into ovuliferous cushions spirally inserted on a continuation of the axis which rises up from the base of the receptacle. Example:—*Hedychium* (figs. 209$^{3, 4, 5}$).

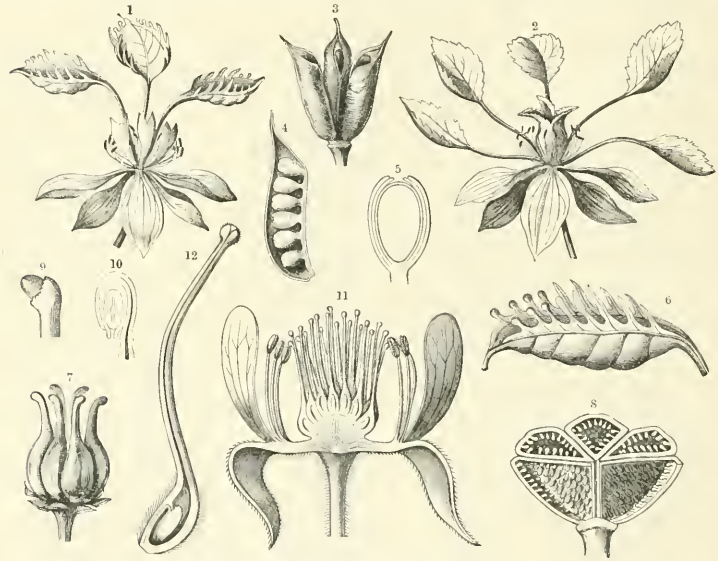


Fig. 210.—Structure of Phanerogamic Ovaries.

$^{1, 2}$ Antholysis or Chloranthy of a Larkspur (*Delphinium cashmirianum*). ^{3} Ripe dehiscing fruit of same. ^{4} Longitudinal section of a single carpel of same. ^{5} Longitudinal section of an ovule of the same. ^{6} A single foliaceous carpel of same. ^{7} Pistil of *Butomus umbellatus*. ^{8} Pistil of same dissected. ^{9} Young ovule of same. ^{10} Full-grown ovule of same in longitudinal section. ^{11} Vertical section of flower of Raspberry (*Rubus Idæus*). ^{12} Longitudinal section of a single carpel of the same. $^{1, 2, 3}$ natural size; $^{4, 6, 7, 11}$ magnified 2-5 times; $^{6, 8, 9, 10, 12}$ magnified 6-8 times.

(17) As before, one series closes the mouth of the receptacle. From the tip of the axis at the base of the receptacle a single apparently terminal carpel arises which bears a single ovule. This condition obtains with many variations in the Compositæ, *e.g.* the Sunflower (*Helianthus*, fig. 207^{5}).

The account of the structure of the ovary just given differs in several fundamental points from the current views of the best authorities in plant morphology. Especially is this so in two points. Firstly, in that the wall of so-called "inferior ovaries" consists, for the most part, according to my own investigations, of a deeply excavated receptacle and not of carpels invested by the tube of the calyx or perianth. That the latter condition occurs (as in many Saxifrages) is not here denied, but more frequently is it the receptacle which is raised as a circular wall to form a closed ovary. On the ripening of the fruit the capsule in many cases opens by means of valves which strikingly resemble the valves formed from true carpels. It is, however, but a resemblance comparable to that existing between the phylloclades of Butcher's-broom and true leaves (*cf.* vol. i. p. 333).

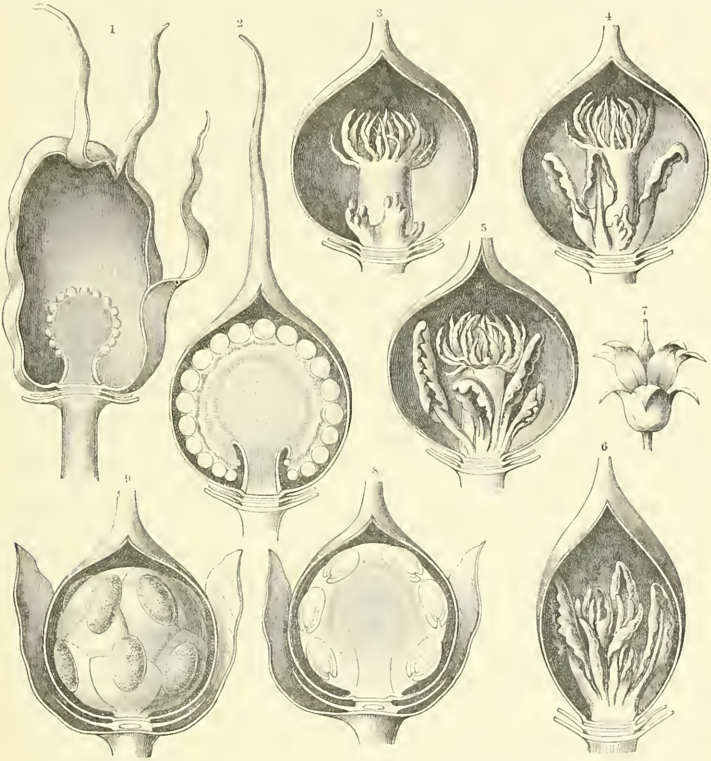


Fig. 211.—Antholysis and Structure of the Ovary.

[1-6] Longitudinal sections of the ovaries of "monstrous" flowers of *Primula japonica*; the outer carpels form the ovarian cavity and are destitute of ovules; the inner carpels show all transitions between ovuliferous cushions, concrescent with the extremity of the axis, and isolated leaf-structures, the marginal teeth of which correspond to ovules. [7] A single "monstrous" flower of *Primula japonica*. [8] Longitudinal section through the ovary of *Glaux maritima*. [9] View into the ovary of same after removal of the front wall. [7] natural size; the others magnified 6–8 times.

A second divergence from recognized views is the assumption that two kinds of carpels take part in the formation of many ovaries, *i.e.* an outer series, destitute of ovules, forming the ovarian cavity, and an inner, ovuliferous series variously metamorphosed into cushions, strings, ridges, &c. This view is supported not only by extensive investigations into the development of ovaries, but also by a number of cases of antholysis which throw considerable light on obscure points of ovarian morphology.

As we shall refer frequently to this state of *Antholysis* it will be well to state at once, briefly, exactly what is meant by the term. Everyone is acquainted with the "double flowers" of Roses, Snowdrops, Carnations, Primroses, Tulips, &c., so common in cultivation. Into the cause of their origin we shall inquire later on; here it is sufficient to note that in double flowers we find (1) that the stamens are entirely or in part transformed into petals, occasionally into carpels; (2) that a multiplication of the perianth-leaves, stamens, and carpels is apparent, and (3) that with this change is often combined a *greening* of the parts not usually green, and (4) a general loosening and separation of parts which in ordinary, single flowers are fused with one another. Especially do we find those leaf-structures which normally are united to form the ovary loosened and increased; they are produced as flattened structures, having much the appearance of green leaves. One finds frequently all possible transitions in one and the same flower, so that the various stages in the conversion of carpels into green leaves can be readily followed.

In cases of antholysis where the parts of the ovary show a transformation into green leaves, one feels justified in regarding the structures in question as foliar in nature. Especially is this so when none of the ascertained facts of development militate against this view. In the same way such parts as never assume the forms of leaves in these "loosened" or segregated flowers may be interpreted as stem-structures—always provided that developmental history harmonizes with this view.

In the cursory review of types of ovarian structure given in the last few pages it was stated that in some cases carpels of one kind only are present, whilst in other cases carpels of two kinds contribute to the formation of the ovary. This statement is based in part on facts gleaned from an examination of these loosened, antholytic, or so-called "monstrous" flowers. The antholytic flowers of a Larkspur (*Delphinium cashmirianum*) reproduced in figs. 210 1-6 show unmistakably that only a single whorl of carpels is present and that each of them bears ovules on its margins. Similarly those of the Japanese Primrose (*Primula japonica*) represented in figs. 211 1, 2, 3, 4, 5, 6, 7, demonstrate that here two sorts of carpels are concerned, *i.e.* outer foliaceous ones destitute of ovules, and inner ovuliferous ones modified into a cushion.

Having described the chief forms assumed by the ovarian cavity, we may pass on to speak of its most important contents, the *ovules*. All ovules agree in this: that at the time of fertilization they consist of masses of tissue, exhibiting a differentiation into central and peripheral cells, and also in the fact that one of the cells of the central portion is destined to become an embryo. In the majority of flowering plants we find a definite central mass of cells, the *nucellus*, surrounded by a well-marked sheath, the coat or *integument*. Generally the integument is double, as in *Delphinium* and *Butomus* (*cf.* figs. 210[5, 9, 10]), in other cases it is single, as in Compositæ, Umbelliferæ, *Hippuris* and *Cycas revoluta* (*cf.* fig. 208[3]). In most Orchids the nucellus is inclosed in a large-celled, inflated and transparent integument, through which it is distinctly visible (*cf.* fig. 212[5]). In not a few epiphytic Orchids, however, this contrast of parts is only imperfectly shown, whilst in the Balanophoreæ and various other parasites no trace of the distinction into nucellus and integument is found. In all cases where an integument is present it is discontinuous at one point, where the nucellus is uncovered. This is the *micropyle*. Sometimes the micropyle is at the apex of the ovule, but in a very large number of cases the whole ovule is bent over so that the micropyle is situated close to the point of attachment of the ovule. The ovule may be attached to its support (*placenta*) by means of a filamentous cord, or it may be directly seated upon it. The common condition of an inverted ovule fused with its filamentous stalk is shown in figs. 208[3] and 210[10]. The filamentous stalk is technically known as the *funicle*, and the ridge where it is fused with the ovule as the *raphe* (*cf.* vol i. p. 644).

The cells of the nucellus of the ovule show a very unequal growth. One of them enlarges in a conspicuous manner, and is known as the *Embryo-sac*. In Conifers it attains relatively to the other cells of the nucellus enormous dimensions, whilst in most other flowering plants as it grows it encroaches upon the other cells of the nucellus till only a single layer remains surrounding it. And even this layer may be in part absorbed, so that the embryo-sac actually penetrates to the micropyle. The protoplasmic contents of the embryo-sac is richly vacuolated, but at the end directed towards the micropyle vacuoles are absent, and the protoplasm breaks up into several distinct protoplasts, each of which is provided with a conspicuous nucleus but in the first instance with no cell-membrane. As a rule three such protoplasts are found at the micropylar end of the embryo-sac; of these one only gives rise, after fertilization, to an embryo. This cell is the *ooplast* or "germinal vesicle", the other two are named *synergidæ* (*cf.* also, figs. 315 and 316).

In the ovaries of Orchids, as shown in figs. 212[1, 2, 3, 4], the ovules arise in great numbers upon peculiar furrowed ridges of the carpels. They arise from the superficial cells of these ridges, and are not provided with any vascular-bundle connections; in fact, they are comparable to those epidermal structures known as hairs or trichomes. This analogy is emphasized by the fact that in the ovaries of many Orchids real hairs are present, as, for instance, in *Lælia Perrinii* and *Cœlogyne plantaginea*, transverse sections of which are represented in figs. 212[1, 2, 3, 4]. In these remarkable species six ridges project from the wall into the ovarian cavity, and from all of these hair-like structures are developed. The three ridges belonging to the curious excavated receptacle, already described, alone bear ordinary unicellular hairs, the others bear ovules, one of which is shown in fig. 212[5].

The ovules of Cycads are very differently developed, as may be seen from a reference to fig. 208 [7]. Here no ovarian cavity is formed, the carpels are distinct from one another, and are spirally inserted upon the termination of the caudex; they are deeply lobed, certain of the segments being transformed into ovules.

Thus, while the ovules of Orchids seem to be equivalent to hairs, those of Cycads represent leaf-segments. In both cases the relations of the parts seem obvious. But in a great many cases the significance of the ovules is by no means so obvious, especially when the developmental history admits of various interpretations. In such doubtful cases antholysis offers a welcome assistance—that is, where this "loosening" and "greening" involves not only the ovary but also the ovules.

Especially valuable in this respect are certain cases of antholysis of the flowers of the Sundew (*Drosera*). Whilst in the normal flowers of this plant the ovules arise on the inner surface of the united carpels, in the foliaceous or antholytic ones they are borne upon the open and isolated carpels as glandular tentacles, like those usually occurring upon the leaves of this plant (*cf.* fig. 212 [6]). On many of the carpels these glandular structures are fused together in little clusters (212 [7]), and these fused structures show various transitional stages leading up to inverted ovules (figs. 212 [8, 9, 10, 11, 12]). From a study of these cases one may infer that the integument of the ovule here is equivalent to a group of tentacles.

Very different is the case of the Larkspur (*Delphinium*). In normal flowers the ovules arise from the infolded margins of the carpels, each of which forms an ovary (*cf.* fig. 210 [4]). But in the foliaceous flower the carpels are open and their margins lobed (*cf.* fig. 210 [6] and fig. 212 [13]). They recall the carpels of Cycas (fig. 208 [7]) and agree with it in that some of the segments are converted into ovules. And it must be especially noted that the leaf-segments are so folded that a pit-like excavation is formed (*cf.* figs. 212 [14] and 212 [15]). Thus it appears that in the Larkspur the ovular integument is formed by the folding of the leaflet-like segments. Different again is the case of the Clover (*Trifolium*), of which an antholysis is shown in fig. 212 [16]. The ellipsoidal ovules, which are borne along the fused margins of the infolded carpel in the normal flower, are here replaced by little, leafy structures resembling leaflets on the margin of the open carpel (*cf.* figs. 212 [16] and 212 [17]). These leafy structures are neither rolled up nor folded, and from each projects the nucellus of an ovule, or rather a mass of tissue corresponding to a nucellus, surrounded by an enveloping wall (*cf.* figs. 212 [18, 19, 20, 21]). This wall may be regarded as representing the inner integument of the ovule, whilst the outer one is replaced by a leaflet. The monstrous ovules in the ovary of the Common Sallow (*Salix Caprea*, fig. 212 [29]) show similar relations, except that the green, leafy structure upon which the nucellus of the ovule is inserted is folded along its midrib and has a fimbriated margin (fig. 212 [30]). Of especial interest are the monstrous flowers of *Rumex scutatus* (*cf.* fig. 212 [24, 25, 26, 27, 28]), a plant common on the débris slopes of limestone mountains. In the normal flower of this plant the ovary is egg-shaped, and consists of three carpels united edge to edge (figs. 212 [22] and 212 [23]). But in these monstrous cases it is enlarged from six to tenfold, and modified into a funnel-shaped tube open above (212 [24, 25, 26, 27]). From this the ovule, also modified into a tube, sometimes

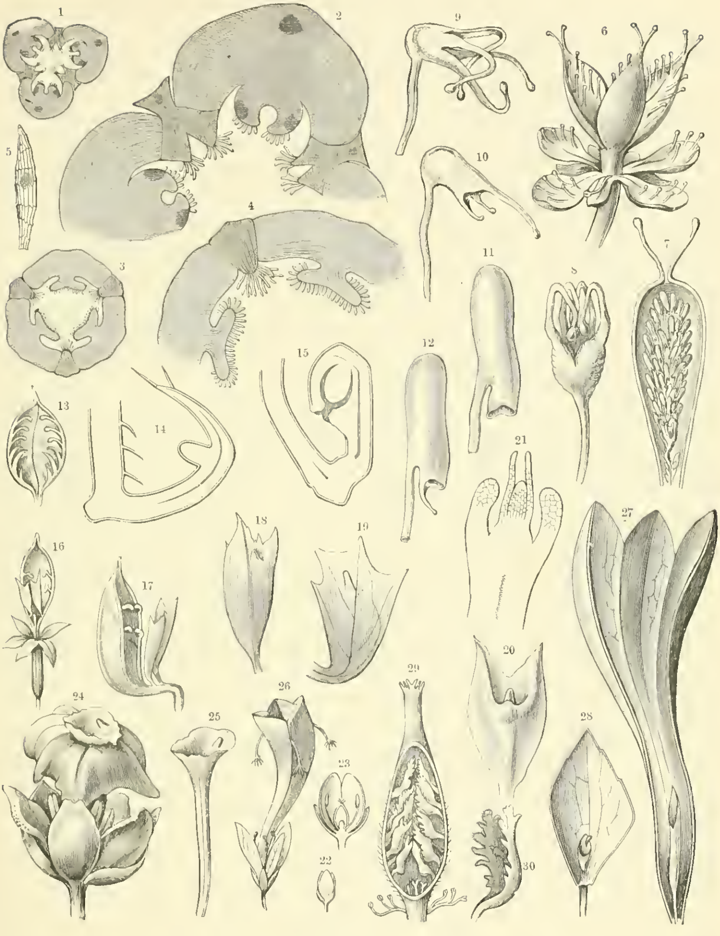


Fig. 212.—Ovules and Foliaceous Carpels.

^{1} Transverse section of the ovary of *Lælia Perrinii*; natural size. ^{2} A portion of this section; ×6. ^{3} Transverse section of the ovary of *Cœlogyne plantaginea*. ^{4} A portion of this section; ×6. ^{5} A seed of *Cœlogyne plantaginea*. ^{6} Antholysis of the flower of Sundew (*Drosera intermedia*). (After Planchon.) $^{7-12}$ Isolated portions of this flower. $^{13-15}$ Isolated portions of a similar flower of *Delphinium elatum*. (After Cramer.) ^{16} Antholysis of *Trifolium repens*. $^{17-21}$ Isolated portions of the same. (After Caspary.) ^{22} Flower of *Rumex scutatus*. ^{23} The same flower in longitudinal section; magnified. $^{24-28}$ Isolated portions from an antholysis of *Rumex scutatus*. (Partly after Peyritsch.) ^{29} Longitudinal section through the pistil of a "monstrous" flower of *Salix caprea*. ^{30} Foliaceous ovule from this pistil. $^{6-30}$ slightly magnified.

projects (212^{24}), or it may remain concealed within (212^{27}). Inside the ovular tube arises a little protuberance which may be regarded as equivalent to the nucellus of the ovule. It is sometimes attached to the wider end of the tube (212 [25]), but more frequently it arises from the narrowed base as a tiny, conical projection inclosed in a circular envelope of its own (212 [28]). This envelope corresponds to the inner, and the tube to the outer integument of the ovule.

From a study of these monstrous flowers it would appear that when the ovule possesses two integuments, the outer one corresponds sometimes to the whole apical portion of a carpel, sometimes to but a segment of a carpel; the former being the case when carpels of two kinds are present, and when, at the centre of the floral receptacle, above the outer non-ovule-bearing carpels, only a single fertile carpel is produced. The inner integument, on the other hand, arises like a corona from the leaf-like outer one.

The nucellus of the ovule arises in many instances (*e.g.* in Orchids) from a mass of tissue produced by the division of a single epidermal cell, but in by far the majority of cases at the margin or upon the surface of a leaf or leaf-segment, resembling in all respects a foliar bud.

That the ovule can be produced directly from the floral receptacle is not yet ascertained with certainty, though such an origin would appear to be not improbable in the Pepper family. That is no good reason why ovules should behave differently from bud-like brood-bodies, which arise sometimes from leaf- and sometimes from stem-structures. So great is the analogy between ovules and detachable buds, that ovules formerly received from Botanists the name of "seed-buds". In this connection it is very instructive to contrast the ovules in the ovary of certain Orchids with the foliar buds produced on the leaves of some of these plants. In *Malaxis paludosa* (*cf.* fig. 200 [5], p. 41) the foliar buds are found partly on the upper surface of the leaf, partly on the margins, forming in the latter case a fringe. They consist of a compact, central portion inclosed in a large-celled envelope which is so fashioned that the whole structure resembles an ovule (*cf.* fig. 200 [6]). So striking is this resemblance, that anyone unacquainted with the fact that these buds arise from foliage-leaves would unhesitatingly regard them as ovules. Later on, of course, differences appear, in that in the ovule an independent embryo is produced, whilst the bud gives rise to a shoot, which must be regarded as a branch of the parent plant. This is, of course, an important distinction, and applicable to the majority of cases, though not quite to all. The parthenogenetically produced brood-bodies, to be treated fully by and by, have both the form of true embryos and occupy the same position in the ovule beneath the micropyle. Were it not known that the hard, indehiscent fruit (achene) of *Gnaphalium alpinum* (= *Antennaria alpina*), with the rudiment of another generation which it contains, is produced without the intervention of pollen, without fertilization, it would certainly not be apparent from its structure. From this we may conclude that the distinction between bud and ovule, between brood-body and fruit, cannot be based on purely structural characters, and that fruits and brood-bodies are sometimes interchangeable—facts of great importance in solving the question of the importance of fertilization in the origin of new species.

STAMENS.

As the last patches of snow disappear from the fields, the Snowdrop raises its white bells, and the catkins of the Willow break through the bondage of their bud-scales; in the copses likewise, where the warm March sunbeams penetrate, the Hazel begins to blossom and sheds its powder. These are the signs that spring is coming, and that the long winter is over. For some time the flowers both of the Snowdrop and Hazel have been ready—in the Snowdrop under ground, wrapped up in sheathing leaves; in the Hazel on the twigs as short, cylindrical, dusky catkins. With the advent of spring the catkins stretch and their crowded flowers are separated, they becoming flexible and hang like golden tassels from the branches, swaying in the wind and giving off their clouds of dust.

To this powder, long known to be connected with the fruiting of plants, the name of flower-dust has been given. This term, suitable in so many cases, has been used in others for a substance which, although corresponding in function to the flower-dust of the Hazel, differs from it in appearance. The cells which take the form of dust in the Hazel assume in other plants the form of sticky, viscous lumps, of spindle-shaped masses or granulated bodies, to which the designation dust is quite inappropriate. Were the species of plants whose flowers do not produce dust but few the term could stand, but when we find belonging to this category many of the principal families of plants—ten thousand Composites, eight thousand Orchids, five thousand Labiates, four thousand Rubiaceæ, three thousand Papilionaceæ, and thousands of Umbellifers, Rosaceæ, Crucifers, &c.; that, roughly speaking, two-thirds of Flowering Plants do not produce dust, it is evident that the term cannot have a general application. Consequently, Botanists speak of *Pollen* and not flower-dust. It is true this word simply means flour, and that its selection has not been a very happy one. Still the term has entered into botanical terminology, where it will remain. It is given to all those cells produced in the flowers of Phanerogams, which contain the spermatoplasm.

Pollen, then, consists of cells which contain spermatoplasm, and may be compared to the antheridia of Cryptogams. A definite portion of the substance of certain leaves of the floral axis is appropriated to the production of Pollen. These leaves, known as *Stamens*, resemble the other leaves of the floral axis in that they are inserted in whorls, or one above the other in a much-flattened spiral. Very few species of plants possess only a single stamen in each flower. The majority of flowers contain stamens arranged spirally or in whorls. As a rule stamens are inserted according to the $\frac{1}{3}$ or $\frac{2}{5}$ system (*cf.* vol. i. pp. 399, 400). In many cases their number and insertion resembles that of the petals and carpels of the same flower, though more frequently there is a difference. Thus, in the flowers of the Tulip-tree (*Liriodendron*), whilst the perianth-leaves have a divergence of $\frac{1}{3}$, the stamens are arranged according to the $\frac{13}{34}$ system. In *Ranunculus* the leaves of the perianth are arranged on the $\frac{2}{5}$ plan, the stamens on the $\frac{8}{21}$; in *Polygonum* the former on the $\frac{2}{5}$, the latter on the $\frac{3}{8}$ system.

Since in every species of plant the number of stamens remains constant, thus in the Mare'stail (*Hippuris*) there is one, in Lilac two, in Iris three, in the Woodruff four, in the Violet five, and in the Tulip six stamens, their number has been made the basis of a classification of flowering plants at once convenient and popular, though not strictly scientific. In the well-known System of Linnæus plants are arranged into groups called Classes, in which the first class (*Monandria*) includes all forms with a single stamen, the second (*Diandria*) those with two stamens, and so on.

The aggregate of stamens in a flower is termed the *Andrœcium*. As a rule the androecium is inserted between the leaves of the perianth and the carpels, so that from without inwards the sequence is perianth, stamens, carpels. Sometimes the carpels are wanting, so that the stamens constitute the inmost members of the flower; similarly also carpels may be present but no stamens.

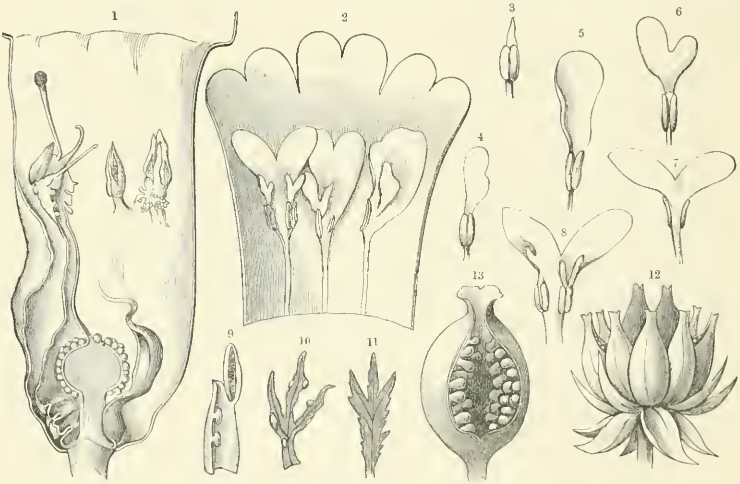


Fig. 213.—Stamens of double and monstrous flowers.

1 Vertical section of a green flower of *Primula japonica*. 2 Vertical section of a double flower of *Primula spectabilis*. 3–8 Isolated stamens from the same flower. 9 Stamen from a green flower of the Tiger Lily (*Lilium tigrinum*). 10, 11 Foliaceous stamens from a flower of *Campanula Trachelium*. 12 Green flower of *Saxifraga stellaris*. 13 A single stamen from the same flower. (All the figures enlarged.)

We distinguish in a stamen that portion which is concerned in the production of Pollen—the *Anther*—and its stalk, the *Filament*. The stamens in many flowers are partly metamorphosed into petals; indeed, there are grounds for believing that all petals have been originally modified from stamens. What are known as "double flowers" are often flowers in which the stamens have given place to petals. All intermediate stages between stamens and petals can be seen in double-flowered Roses, Carnations, and Primulas (*cf.* figs. $213^{3, 4, 5, 6, 7}$). Not infrequently, at the place where a petal narrows into its stalk or "claw", a little yellow swelling or callosity may be seen; this may be regarded as a reduced anther, and now and then it possesses the character of an anther, and contains actual pollen. It is frequently observed in double flowers that a multiplication of the leaf accompanies the conversion of stamens into petals. In the place of a single stamen we may find two stamens partially converted into petals, or there may be a greater number of petal-like leaves, standing one behind another, or, finally, we may have the appearance shown in figs. 213^{2} and 213^{8} of a double Primula.

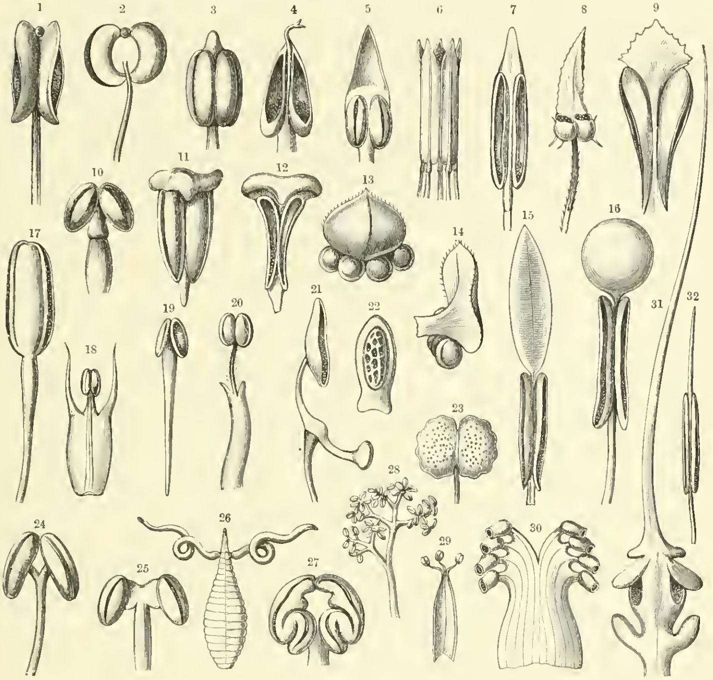


Fig. 214.—Stamens.

^{1} *Empleurum serrulatum.* ^{2} *Hypericum olympicum.* ^{3} *Juglans regia.* ^{4} *Soldanella alpina.* ^{5} *Viola odorata.* ^{6,7} *Artemisia Absynthium.* ^{8} *Haminia* (after Baillon). ^{9} *Abies excelsa.* ^{10} *Euphorbia canariensis.* ^{11,12} *Platanus orientalis.* ^{13,14} *Juniperus Sabina.* ^{15} *Halicmocnemis gibbosa.* ^{16} *Halantium Kulpianum.* ^{17} *Sanguinaria canadensis.* ^{18} *Allium sphœrocephalum.* ^{19} *Actœa spicata.* ^{20} *Aconitum Napellus.* ^{21} *Salvia officinalis.* ^{22} *Viscum album.* ^{23} *Mirabilis Jalapa.* ^{24} *Tilia ulmifolia.* ^{25} *Thymus serpyllum.* ^{26} *Acalypha* (after Baillon). ^{27} *Bryonia dioica.* ^{28} *Ricinus communis.* ^{29} *Corydalis capnoides.* ^{30} *Polygala amara.* ^{31} *Doryphora* (after Baillon). ^{32} *Paris quadrifolia.* (All figures somewhat enlarged.)

By the action of parasitic Aphides and Insects stamens often assume a leaf-like appearance, they become green like the carpels described on p. 80. Such instances are of value in comparing the various parts of a stamen with those of the hypothetic fundamental type of leaf-structure. At the first glance it might be supposed that the filament is a metamorphosed petiole, and the anther a metamorphosed lamina. But these monstrous flowers seem to indicate that such is comparatively rarely the case. Thus in the green stamens of *Campanula Trachelium* (figs. 213^{10} and 213^{11}) there are scattered everywhere over the green substance of the lamina yellow excrescences and warts containing reduced pollen-cells, and occasionally these occur fused together into actual portions of anthers; hence it may be inferred that in this case the anther may be regarded as equivalent to a green lamina. But far more frequently in such cases the pollen-producing tissue is found at the *base* of the lamina only, at the upper extremity of the leaf-stalk, where these two parts articulate. From this we may conclude that in the majority of cases anthers correspond to that portion of a leaf at which the stalk runs into the lamina. In such stamens the lamina is entirely suppressed, or is represented by a continuation above the pollen-producing region.

A few forms of this continuation above the anther, which we regard as representing a leaf lamina, are illustrated in fig. 214. Figs. 214^{1} and 214^{2} show it as a small shot-like grain, 214^{3} as a truncate cone, 214^{4} as a two-pronged fork, $214^{5, 6, 7}$ as a flat, triangular scale, 214^{8} as a toothed, sword-shaped process, $214^{9, 11, 12, 13, 14}$ as a curved membraneous scale, 214^{15} and 215^{16} as a coloured bladder for attracting insects; and, finally, figs. 214^{31} and 214^{32} as a long, whip-like bristle.

That the filament of the stamen, or at any rate its lower portion, corresponds to a leaf-stalk seems so obvious, that it is hardly necessary to prove it by comparison with monstrous cases. Its name of *filament* indicates its character in a great number of flowers. Examples of these are Hemp, Hop, Wheat, Rye, Rice, Maize, Flax, and many others. For many cases no doubt the term filament is unsuited, as, for instance, in the thick, abbreviated stalks in the Violet and Bryony (figs. 214^{5} and 214^{27}). Similarly the filament may be strap-, spindle-, or club-shaped. The last is the case in *Thalictrum aquilegifolium*, *Bocconia*, *Sanguinaria*, and *Actæa spicata* (*cf.* figs. 214^{17} and 214^{19}), and it has been observed that the stamens very readily oscillate at the moment of liberation of pollen with the slightest breath of air. Like the foliage-leaves of the Orange, the stalks of which are provided with a peculiar joint, many Spurges and Labiates have hinged filaments (*cf.* figs. 214^{10} and 214^{21}). These hinges are wonderfully fashioned in many species of *Salvia*, reminding one of the articulation of the feet of insects; their importance in fertilization will be described in a later chapter. In the Linden the filament forks immediately below the anther (fig. 214^{24}), whilst in *Corydalis* it is band-like, and divides into three (fig. 214^{29}). In the Castor Oil Plant (*Ricinus*), and many other Euphorbiaceæ, it is much divided and branched (fig. 214^{28}). These *divided* filaments are not to be confused with *fused* ones, for occasionally we find that the filaments of adjacent stamens unite with one another into a ribbon or tube, as for instance in Mallows, Papilionaceæ, and Polygalaceæ (*cf.* 214^{30}).

Attached to the sheath of foliage-leaves curious appendages, the stipules, are often found (*cf.* vol. i. p. 595). In the case of stamens these are but rarely met with. They occur, however, in certain species of Ornithogalum (e.g. *Ornithogalum nutans* and *chloranthum*), in *Allium rotundum* and *sphærocephalum*, and in the Monkshood (*Aconitum*). Occasionally such staminal stipules are modified as honey-secreting glands at the base of the stamen, *e.g. Doryphora* (*cf.* figs. 214[18] and 214[20]).

It sometimes happens in monstrous flowers that the stamens are transformed into carpels, or we may find here and there an isolated stamen, which is partly so modified and partly still polliniferous. In such monstrosities it usually happens that it is the upper part which forms pollen, and the lower part which produces ovules (*cf.* figs. 213[1] and 213[9]). From this and other facts it has been inferred that the ovary corresponds really to the sheaths, the style to the petioles, and the stigma to the laminæ of the floral-leaves concerned. The monstrous flower of a Saxifrage (figs. 213[12] and 213[13]) shows that anthers and ovules can be produced from the same part of the leaf-stalk. This flower (213[12]) produces at the periphery five sepals and five narrow, green petals; in the centre two carpels (shaded dark in fig. 213[12]) as in normal Saxifrage flowers. Between the petals and carpels, *i.e.* where the stamens are usually found, there are ten structures which, whilst resembling both carpels and stamens to some extent, remind one forcibly of the excavated leaf-rachis of so many of the Pitcher Plants (*cf.* vol. i. pp. 125–133.) One of these is represented in fig. 213[13]. Its free extremity consists of an irregularly serrated scale, which may be compared either to a stigma or to the continuation of an anther, and may be regarded as the metamorphosed lamina. The excavated portion below may be regarded as the petiole. In its cavity are four rows of yellow protuberances, which might at first sight be taken for ovules. Closer investigation shows, however, that they contain pollen-mother-cells, each inclosing four pollen-grains. Here, then, we find the petiole consisting partly of carpel and partly of anthers, from which it may be concluded that that portion of the carpel which produces ovules corresponds entirely in position to the pollen-producing tissue.

The parts of the anther which produce Pollen in special chambers are known as *Pollen-sacs*, the tissue which binds these together as the *connective*. The connective is a direct continuation of the filament, and, like this, is penetrated by a vascular bundle. The pollen-sacs may be arranged like niches around the columnar connectives, which itself terminates in a sort of little shield, as in the Yew Tree (*cf.* fig. 234[2]), or they may be situated symmetrically right and left of it. In the latter case the pollen-sacs may lie at the edge of the connective in one place, as in the Juniper (figs. 214[13] and 214[14]), or they may be in pairs, *i.e.* two pollen-sacs to the right and two to the left of the connective (fig. 214[3]). This latter form is by far the most frequent, and occurs in certainly 90 per cent of all Phanerogams. It must be pointed out that the two pollen-sacs of each pair are separated from one another by a partition-wall only in the young anther. This disappears later on, and in the mature anther one finds, instead of four, only two sacs filled with pollen. Sometimes all four pollen-sacs run together in this way, by the breaking down of the parti-walls, as in Sundew (*Drosera*), Moschatel (*Adoxa*), *Monotropa,* and especially in *Globularia* (*cf.* figs. 216[27] and 216[28]). In

Orchids, on the other hand, the number of pollen-sacs is reduced to two, a number which remains unaltered at maturity.

The pollen-sacs in the anthers of the Mimoseæ are very curiously formed. In the anthers of *Acacia, Albizzia, Calliandra,* and *Inga,* there are eight spherical chambers in which pollen is produced, whilst in *Parkia* we find longitudinal rows of lenticular cavities in which balls of pollen lie embedded. The anthers also of the Rhizophoreæ show several longitudinal rows of such chambers, amounting in all to as many as thirty. The anthers of the Mistletoe (*Viscum,* fig. 214[22]) contain as many as forty to fifty pollen-chambers. In the majority of the Laurels (Lauraceæ) each anther is divided into four cavities, which stand in pairs, one above the other. As a rule, all four open towards that side by which insects visiting the flower for honey have to pass.

Many marked variations in the form of the anther are due to the relative dimensions of connective and pollen-sacs. Thus in the majority of Ranunculaceæ, Magnoliaceæ, Nymphæaceæ, and Papaveraceæ, the connective is broad, the pollen-sacs forming only a narrow rim to the anther (*cf.* fig. 214[17]). In the Skull-cap (*Scutellaria*), Calamint (*Calamintha*), Thyme (*Thymus*), and many other Labiates, as also in several Rosaceæ (*Rosa, Agrimonia,* &c.), the connective has the form of a three- to six-sided mass of tissue in which are embedded the spherical or egg-shaped pollen-sacs. Such anthers frequently resemble an insect's head with two lateral eyes. It is not always possible to distinguish the limits of connective and filament, the whole stamen resembling a truncate column or anvil (figs. 216[26] and 216[32]).

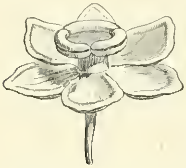


Fig. 215.—Curved anthers in the flower of *Phyllanthus Cyclanthera* (after Baillon).

Sometimes the connective assumes the form of a bar or lever running transversely to the filament, to which it is attached by a movable joint. This is notably the case in certain species of *Salvia,* to be described hereafter. Such a connective moves very readily upon its fulcrum. In many Liliaceæ (*e.g.* Tulips, Lilies, and Crown Imperials) and several Gentians (*Gentiana ciliata, nana,* &c.), the anther is united with the filament by an extremely delicate joint, so that the slightest touch sets it in vibration (versatile anthers). As examples of bulky pollen-sacs and much reduced connective, *Mirabilis Jalapa* (fig. 214[23]) and *Solanum Lycopersicum* (fig. 216[2]) may be quoted as examples.

It stands to reason that the character of the anther, indeed of the whole stamen, is correlated with the form of the pollen-sacs. All possible stages occur between globular and egg-shaped, and between egg-shaped and linear pollen-sacs. The drawings of sixty-four different stamens in figs. 214 and 216 give a good idea of the variety in this respect. Very curious are the curved anthers of *Phyllanthus Cyclanthera* (fig. 215), and those of *Acalypha,* which resemble a ram's horns (fig. 214[26]); the same remark applies to the undulating anthers of many Cucurbitaceæ, of which those of *Bryonia dioica* may serve as an example (fig. 214^{27}). There are forms allied to this last-named plant in which the anthers show very complicated convolutions—like those of the human brain.

When the time draws near for the pollen to leave its place of origin, its cells—whether in a loose powder or sticking one to another—become free from the inclosing wall of the anther, and lie embedded in the cavity of the pollen-sac, as it were in a purse or pocket, awaiting their release. The pollen-sac, hitherto closed, now opens, and the pollen is liberated. This opening or *dehiscence* of the pollen-sacs is accomplished in various ways. It has been already explained that most young anthers contain four sacs which rarely all remain distinct, but, by the breaking down of the parti-walls between each pair, become merged into two cavities.

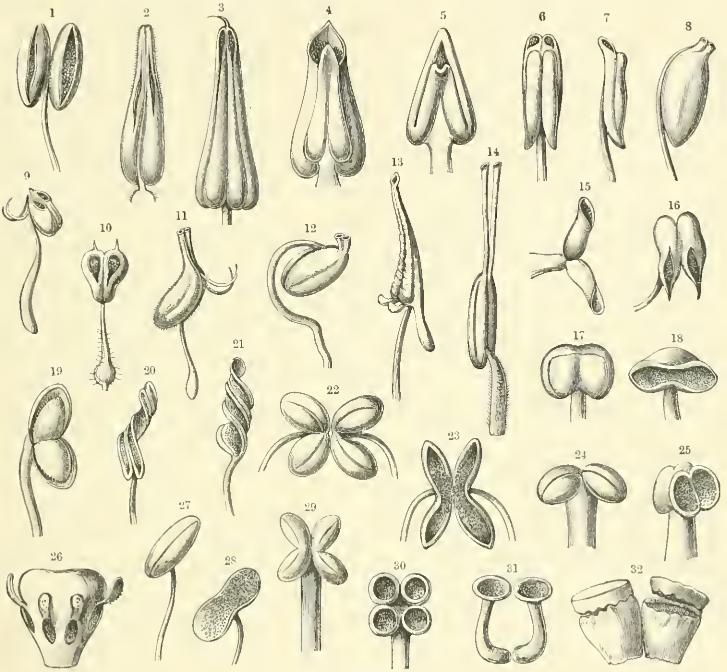


Fig. 216.—Stamens.

^{1} *Calandrinia compressa.* ^{2} *Solanum Lycopersicum.* ^{3} *Galanthus nivalis.* ^{4} *Cyclamen europæum.* ^{5} *Ramondia pyrenaica.* ^{6}, ^{7} *Cassia lenitiva.* ^{8} *Pyrola rotundifolia.* ^{9} *Arctostaphylos Uva-ursi.* ^{10} *Arctostaphylos alpina.* ^{11} *Vaccinium uliginosum.* ^{12} *Pyrola uniflora.* ^{13} *Medinilla* (after Baillon). ^{14} *Vaccinium oxycoccus.* ^{15} *Calceolaria Pavonii.* ^{16} *Tozzia alpina.* ^{17}, ^{18} *Sibbaldia procumbens.* ^{19} *Galeopsis angustifolia.* ^{20}, ^{21} *Erythræa Centaurium.* ^{22}, ^{23} *Melissa officinalis.* ^{24}, ^{25} *Calla palustris.* ^{26} *Nyctandra* (after Baillon). ^{27}, ^{28} *Globularia cordifolia.* ^{29}, ^{30} *Theobroma Cacao.* ^{31} *Pinguicula vulgaris.* ^{32} *Garcinia.* (All somewhat enlarged.)

These two cavities may be spoken of as anther-halves. In cases where the four cavities remain distinct, a curious aperture is formed above each of them, as, for instance, in *Theobroma Cacao* (figs. 216^{29} and 216^{30}). When, however, the aforesaid fusion takes place (e.g. *Calla palustris*, figs. 216^{24} and 216^{25}), two openings only are formed. The anthers of *Globularia* have a very small punctiform connective and four pollen-sacs joined into an ellipsoidal body. After the disappearance of the parti-walls, leaving a single cavity occupied by pollen, a gaping, transverse slit arises, so that the anther is transformed into an open vessel (*cf.* figs. 216^{27} and 216^{28}). After the removal of the pollen the remains of the original parti-walls can be distinguished as two intersecting ridges. Similarly in the Butterwort (*Pinguicula*, fig. 216^{31}) and in the majority of so-called one-celled anthers. In many Labiates, in which the anthers of adjacent stamens are in contact, and to some extent united together (syngenesious), the openings of the pollen-sacs in each anther unite, with the result that a pair of somewhat sinuous niches are presented, borne on the two curved filaments (*cf.* figs. 216^{22} and 216^{23}).

Dehiscence is accomplished sometimes by the formation of holes or pores, sometimes by slits. Of anthers with *porous dehiscence*, the greatest variety is exhibited by the Heath tribe and Pyrolaceæ. In the anthers of the Bilberry, Bog Vaccinium, Cowberry, and Cranberry (*Vaccinium Myrtillus, uliginosum, Vitis-idæa, Oxycoccos*), as also in Winter-green (*Pyrola*), the pouch-like pollen-sacs are drawn out into shorter or longer tubes, each of these tubes opening at its extremity by small circular pores (*cf.* figs. $216^{8, 11, 12, 14}$). But much more frequent is a dehiscence by means of *slits*. These are either longitudinal or transverse, or they may be sinuous or semicircular. When they are semicircular a valve or trap-door is cut out of the anther-wall.

At its first formation the slit resembles one cut by a sharp knife (*cf.* fig. 216^{1}). In a number of cases the margins of the slit remain together, so that the aperture retains the form of a narrow crack; more frequently, however, the slit gapes, its margins roll up outwards or are folded back like a lid or folding-door. The *longitudinal slits* reach from end to end of the pollen-sacs (fig. 216^{1}), or they may take the form of short gaping clefts near the free extremity of the anther. In the latter case (several examples of which are represented in figs. $216^{2, 3, 6, 7, 9, 10, 13, 15, 16}$), the slits very much resemble pores, from which they can only be distinguished in some cases by their mode of development. Occasionally the short, gaping clefts of adjacent anther-halves unite into a single opening, with a heart-shaped or rhomboidal outline, by which the whole of the pollen of both anther-halves escapes (examples are *Cyclamen* and *Ramondia*, figs. 216^{4} and 216^{5}). *Transverse slits* are met with most frequently in the stamens of Euphorbiaceæ, Cyclanthaceæ; also in a few Rosaceæ (*Alchemilla* and *Sibbaldia*, figs. 216^{17} and 216^{18}), in the Golden Saxifrage and Moschatel (*Chrysosplenium* and *Adoxa*), in *Globularia*, *Malva*, and others. On the whole, however, this method of dehiscence is rare. Of still rarer occurrence is that form of dehiscence in which semicircular slits arise in the anther-wall, producing valves or trap-doors. This is known as *valvate dehiscence.* It is met with generally in Berberidaceæ (e.g. *Berberis* and *Epimedium*) and Lauraceæ. In the Bay Laurel, Camphor, and Cinnamon Trees (*Laurus nobilis, Camphora officinalis,* and *Cinnamomum*) and *Nyctandra* (fig. 216 [26]) are found little apertures on one side of the stamen, each with its trap-door or valve, which is raised up in dry, but shut down in wet weather. The anthers of *Mimulus, Galeopsis,* and *Garcinia* (figs. 216 [19] and 216 [32]) resemble little tubs or boxes, which on opening raise their lid-like valves.

The dehiscence of the anthers in many plants is accompanied by yet other changes. The two anther-halves may become partly separated from their attachments and become twisted or diverge at right angles. If the anther-halves separate at the base only, as in *Convolvulus, Gentiana,* and *Menyanthes,* the anther assumes the form of an arrow-head; if they separate both above and below, and at the same time become somewhat bent, we have an X-shaped anther, found in many Grasses. In many Crucifers (*Diplotaxis, Sinapis,* &c.) the anthers become spirally twisted after dehiscence, a feature very pronounced in the Centaury (*Erythræa,* figs. 216 [20] and 216 [21]). A very striking phenomenon is the shortening which not a few anthers with longitudinal slits undergo after dehiscence. The anthers of most Liliaceous plants are long and linear; they dehisce by means of slits from above downwards. In the course of a few hours they are transformed into globular bodies, covered with pollen. In *Gagea lutea* these balls have a diameter only one-third of the previous length of the anther, whilst the anthers of the Crown Imperial (*Fritillaria imperialis*) shorten from 20 to 10, those of *Narcissus poeticus* from 11 to 4, and those of *Scilla bifolia* from 2 to 1 millimetres.

Each one of the various occurrences which accompany or succeed dehiscence depends upon some structural character of the anther-wall. The relations are simplest in those anthers which open by means of pores. The pores arise from the absorption of limited portions of the wall. Further changes, such as the shrivelling or shortening of the anther, or the expanding of the apertures, do not occur. There is a corresponding simplicity of the tissues of the anther-wall. Similarly, in anthers (*e.g.* Orchids) in which a splitting arises along a previously-indicated line, or in consequence of the absorption of a row of cells, no peculiarities are noticeable on the wall. But where slits with movable lips and valves are developed, cells of characteristic structure are present, which may be termed the contractile cells. One series consists of more or less cubical cells, and exhibit, on portions of their walls, fibrous or rod-shaped thickenings. The wall of one of these cells directed towards the cavity of the anther is equally thickened, that towards the outside is thin and delicate, easily folded, and destitute of thickenings. The side-walls, however, are characteristically strengthened by rod-like thickenings. The thickenings present may be compared to a hand, in the position usually employed in grasping an apple; the palm corresponds to the strongly-thickened inner wall, and the fingers to the tapering, rod-like thickenings of the side-walls. As the cells dry a contraction of the rod-like thickenings supervenes, leading to a movement like that of the afore-mentioned hand when the tips of the fingers approach one another. Simultaneously the thin outer walls are thrown into folds, so that where a number of these cells are present, side by side, the whole outer surface will contract. These cells, being appropriately distributed over the wall of the anther, will cause the slit-margins to fold back or the valves to be raised. Besides these, other forms of contractile cells are present, differing from those described chiefly in form rather than in their mode of action.

It must suffice here to mention only a very few instances. The anther-wall in Conifers consists of a single layer of contractile cells, whilst that of *Agave* reaches the other extreme, there being six to eight layers of such cells present. As a rule the contractile layer is covered externally by a layer of delicate, thin-walled cells, known as the *Exothecium*; the contractile layer constitutes the *Endothecium*. The lining of the pollen-chambers consists of yet a third layer, the *tapetal cells*. In anthers which have dehisced this last-mentioned layer is rarely demonstrable, it having been already absorbed. Of the various layers it is the middle one, the endothecium (contractile cells), which is active in the various movements under discussion.

In the discharge of the pollen from the opened anthers a great variety of methods prevails. In the Nettle and Mulberry the filament of the stamen uncoils like a spring at the moment of dehiscence of the anther, and the pollen is forcibly scattered (fig. 229). The whole event is instantaneous, and to the observer resembles an explosion. In other plants dehiscence is accomplished quietly, and the pollen, which escapes slowly, may be first of all stored up temporarily at definite spots within the limits of the flower. This storage occurs a good deal more frequently than is generally supposed, and stands in relation to various events which will be fully discussed later on. In Papilionaceæ the liberated pollen is deposited in the hollowed apex of the *Keel*; in the Violet it is stored in the grooves of the lowest, spurred petal; in the Poppies, Roses, and Buttercups, it falls, at any rate in part, on to saucer-like depressions of the petals. The dust-like pollen as it falls from the anthers of the catkins of the Walnut, Hazel, Birch, and Alder, is received temporarily on the upwardly-directed under-surfaces of the flowers standing below (*cf.* fig. on p. 742, vol. i.). In Composites, Campanulas, and several Stellatæ, the pollen is stored on the style or stigma, but not, as was previously supposed, upon the receptive portions of this organ. On the contrary, it is retained here by various hairs and papillæ, specially designed for the purpose. Then, in the Proteaceæ again, the pollen is deposited, whilst the flower is still in bud, upon the summit of the stigma, without, however, coming into contact with the receptive spot; the stigma in this case serves, at the commencement of flowering, as a temporary depôt for the pollen. In Sarracenia the pollen falls upon the stigma, which has the form of an expanded umbrella, and here for a while it remains, but not in contact with the receptive points. We shall hardly overstep the mark in saying that in some 20,000 species of plants the pollen is temporarily stored in some portion of the flower and preserved for future use.

More frequently, however, the pollen remains within the opened anther. Usually these flowers are visited by insects which disturb the anthers and release the pollen, or they dust themselves over with it and carry it off to another flower.

The fact that the anthers are directed sometimes inwards, sometimes outwards, is correlated with these insect-visits. Where the slits or pores of the anthers are directed towards the periphery of the flower, one speaks of outwardly-directed anthers (extrorse), where toward the centre of the flower, of inwardly-directed (introrse). These relations are of importance in respect of insect-visits. If the honey is situated outside the whorl of stamens, the insects must pass between the stamens and petals to secure the nectar, as in *Colchicum*, *Iris*, *Convolvulus*, *Epimedium*, and *Laurus*. Here it will be advantageous for the anthers to be extrorse. On the contrary, when the honey is between the ovary and the bases of the stamens, and the insects have to penetrate to this region, as in Gentians and Opuntias, the stamens will be introrse. It is of great importance that the pollen exposed in the anthers should be rubbed off by the insects and carried to other flowers, a result only obtainable when the dehiscent side of the anther is placed in the way of the insect as it enters or leaves the flower.

Numerous other peculiarities affecting the structure, position, and movements of stamens will be dealt with later on, when treating of the removal of pollen from and to flowers by insects and other animals.

POLLEN.

Like all other leaf-structures, stamens arise in the first instance as convex projections from their points of insertion on the stem. These projections consist of a homogeneous, small-celled tissue. They soon, however, assume a club-shaped form, and the outlines of anther and filament become recognizable. A vascular bundle is found traversing the entire length of each stamen, and the anther, which increases in size more rapidly than the filament, shows symmetrically-arranged, longitudinal grooves, with projecting portions between, arranged in pairs. The cells situated immediately below the surface of the young anthers become now marked out into tissues of two kinds. Towards the outside three layers of cells become distinguishable, and these, with the outermost, enveloping layer give rise to the wall of the anther; within, large cells become conspicuous, and form what is known as the *archesporium*.

These archesporial cells are arranged either in nests or in longitudinal rows embedded in the surrounding tissue. In the latter, the more usual, case, there are four, rarely two or eight, such rows arranged in pairs right and left of the central vascular bundle. Although at this stage of development all the cells of the anther hang together into a continuous mass, the existence of the future pollen-sacs—now filled with the archesporial cells—is easily recognized. As time goes on the contrast between the wall of the anther and the contents of the chambers becomes more pronounced. The archesporial cells divide, giving rise to the pollen-mother-cells which entirely fill the pollen-sacs. Of the layers of the anther-wall, the inmost is usually dissolved, so that the mother-cells are bathed in a fluid mucilage; thus the wall comes to consist solely of the outmost, enveloping layer and of the contractile cells ("fibrous layer") within.

Changes continue in the chambers or pollen-sacs, and in the partition-walls between them. The walls of the pollen-mother-cells become thickened, and often show a stratification. The protoplasm within divides into four parts, arranged frequently, though not invariably, in the corners of a 4-sided pyramid (*i.e.* in tetrads). Each of these cells becomes invested with a wall of its own, at first thin and delicate, but afterwards thickened and stratified. These are the pollen-grains. Their protoplasm possesses the property of a fertilizing agent, and is termed the *Spermatoplasm.*

In most plants a further division of the protoplasm in the pollen-cells takes place. This is conspicuous in the Conifers and Cycads, but relatively obscure in the majority of flowering plants. Of the two or more cells thus arising within the pollen-grain one only takes an actual part in fertilization.

How long the spermatoplasm retains its fertilizing properties unimpaired has not been sufficiently investigated. It has been stated of the plants enumerated below that this property is lost as follows:—

In *Hibiscus Trionum*	after 3 days.
„ The Wallflower (*Cheiranthus Cheiri*)	„ 14 „
„ „ Pansy (*Viola tricolor*) ...	„ 26 „
„ „ Bugle (*Ajuga reptans*) ...	„ 32 „
In the Larger Periwinkle (*Vinca major*)	after 43 days.
„ *Pæonia pubens*	„ 58 „
„ *Pæonia tenuifolia* ...	„ 65 „
„ *Clivia nobilis*	„ 76 „

It is by no means an unusual thing for gardeners to send the pollen of Cycads and Palms for fertilization to distant countries without its properties being impaired, provided it is kept dry during transit. The Arabs, who artificially pollinate the female flowers of the Date-palm, put aside some of the pollen from year to year, so that, in the possible event of the male flowers not developing, they may ensure a crop of dates. According to tradition, the pollen of Date-palms, Hemp, and Maize, can be used effectively for artificial pollination even after a lapse of eighteen years. Unfortunately, reliable investigations are wanting to show whether these accounts belong to the realm of gardeners' stories or not.

A great diversity obtains as to the manner of coherence of the pollen. When the walls of the mother-cells, containing the pollen-grains, become entirely absorbed, the pollen-sacs are filled with isolated cells, a condition which may be described as *free pollen.* Even now numbers of adjacent pollen-grains may cohere in clusters, in consequence of their possessing sticky coats or other arrangements. But in this case there is no suggestion of its being a real tissue, a difference of some moment.

In many plants, on the other hand, the pollen-cells remain, as they arose in the mother-cells, united together in fours, and in this condition they leave the anther-cavities. These little pollen-aggregates are termed *tetrads*. Examples of such plants are:—the Ericaceæ (*Erica, Calluna, Menziesia, Andromeda*), the Bearberry (*Arctostaphylos*), the Strawberry Tree (*Arbutus*), the Alpine Rose (*Rhododendron*), *Ledum, Kalmia*, the Cranberry and Bilberry (*Vaccinium*); the Epacridaceæ, *Epacris* and *Leucopogon*; many Winter-greens (Pyrolaceæ); a few Sedges (*Juncus Jacquinii* and *Luzula vernalis*); finally *Anona, Drimys, Jussieua*. In the plants just enumerated the tetrads correspond to the four pollen-cells in the corners of the mother-cell (*cf.* fig. 219^2); but in the Apocynaceæ (*Apocynum, Periploca*), in numerous Orchids (*Ophrys, Spiranthes*), in *Fourcroya* (nearly related to *Agave*), and in several Bulrushes (*Typha Shuttleworthii* and *latifolia*), the four pollen-cells are arranged in one plane. In a few Willow-herbs (*e.g. Epilobium montanum* and *hirsutum*) the four cells are joined, but so slightly that they are readily separated on pressure.

Of much rarer occurrence than tetrads are *pollinia*. This name is given to the resultant mass of pollen-cells, when the whole of the pollen produced from a single archesporium (*i.e.* the whole contents of a pollen-sac) remain joined together into a tissue. A pollinium may consist of 8, 12, 64, or even many hundreds of pollen-cells. In the Mimoseæ the pollinia, which are found serially arranged, are lenticular, egg-shaped, or globular in form; in the Asclepiads they are spatulate, and consist of hundreds of pollen-cells. The pollen-masses of many Orchids are built up of numerous little clusters of pollen-cells, and show a branching or lobing; each of these clusters or lobes consists of greater or smaller pollinia. The masses, into which the pollinia of Orchids are aggregated, usually terminate in a stalk which is attached at its other end to a disc. This disc is so sticky that it readily adheres to any object coming in contact with it—a fact of significance in the conveyance of the pollinia from flower to flower by insects.

The dimensions of pollen-grains are very various in different groups of plants. Thus, whilst in the Forget-me-not (*Myosotis*), Borage (*Borago*), Comfrey (*Symphytum*), and Boragineæ generally, as also in Artocarpeæ (e.g. *Ficus*), the pollen-grains are very small, in Cannaceæ, Malvaceæ, Cucurbitaceæ, and Nyctagineæ, they are relatively large. The following table of diameters of pollen-grains shows the variation which exists in this respect:—

	Millimetres.		Millimetres.
Myosotis alpestris,	0·0025–0·0034	*Viola tricolor*,	0·062–0·071
Lithospermum affine,	0·0042–0·0052	*Convolvulus sepium*,	0·076–0·084
Ficus pumila,	0·0045–0·0056	*Geranium Robertianum*,	0·085–0·094
Carinthe minor,	0·0050–0·0057	*Opuntia cynanchica*,	0·15 –0·20
Echium vulgare,	0·010 –0·014	*Oxybaphus nyctagineus*,	0·18 –0·22
Pilea microphylla,	0·018 –0·020	*Morina Persica*,	0·19 –0·24
Rhamnus cathartica,	0·022 –0·032	*Cucurbita Pepo*,	0·20 –0·23
Syringa vulgaris,	0·024 –0·034	*Mirabilis longiflora*,	0·20 –0·24
Aloe denticulata,	0·035 –0·050	*Cucumis Melo*,	0·20 –0·24
Yucca angustifolia,	0·055 –0·065	*Mirabilis Jalapa*,	0·22 –0·25

The pollen-grains of the Marvel of Peru (*Mirabilis Jalapa*) are consequently a hundred times greater than those of the Alpine Forget-me-not (*Myosotis alpestris*). It appears also that in many flowers which remain open but a single day or night, as, for instance, the Gourd and Melon, *Portulaca*, *Morina*, and the various species of *Mirabilis*, the pollen-grains are especially big. In a single anther-cavity of *Mirabilis Jalapa* there are, on the average, 32, and in one of *Borago officinalis* 60,000 pollen-grains.

In form pollen-grains are generally ellipsoidal (*cf.* figs. 217^{13} and 217^{14}), at any rate in quite half of all flowering plants. More rarely are they spherical (figs. $217^{1, 3, 4, 6, 7}$). In the liliaceous *Tritelia* they are narrow and lancet-shaped, and in *Morina* (fig. 217^{2}) biscuit-shaped. In the Pine the pollen-grain possesses two hemispherical bladders, and resembles an insect's head with two huge eyes (fig. 217^{8}). In *Crucianella latifolia* they are barrel-shaped, and in *Brugmansia arborea* shortly cylindrical. Next to the ellipsoidal form, the angular or crystalline is the commonest. Thus the pollen-grains of the Nasturtium (*Tropæolum*) are 3-sided prisms, those of the Pansy (*Viola tricolor*) 4 or 5-sided, and those of Lady's

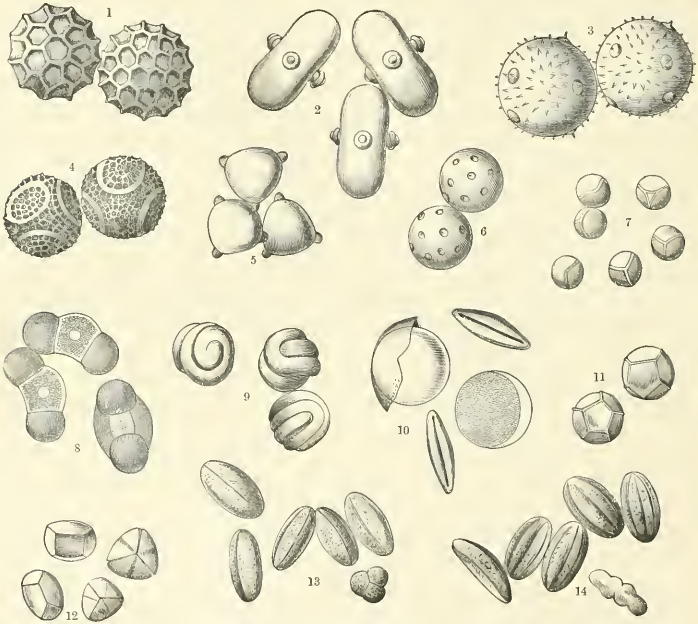


Fig. 217.—Pollen-grains.

^{1} *Cobœa scandens.* ^{2} *Morina Persica.* ^{3} *Cucurbita Pepo.* ^{4} *Passiflora Kermesina.* ^{5} *Circæa alpina.* ^{6} *Convolvulus sepium.* ^{7} *Cannabis sativa.* ^{8} *Pinus Pumilio.* ^{9} *Mimulus moschatus.* ^{10} *Albucca minor* (dry and moistened). ^{11} *Dianthus Carthusianorum.* ^{12} *Corydalis lutea.* ^{13} *Gentiana rhætica.* ^{14} *Salvia glutinosa.* $^{1-3}$ ×80–90; $^{4, 6, 7, 8, 10}$ ×120–150; $^{11, 12}$ ×180; $^{6, 9, 13, 14}$ ×220–250.

fingers (*Anthyllis vulneraria*) short 6-sided prisms with striated angles. A cubical form obtains in the pollen-grains of *Triopteris brachypteris* and *Basella alba*, that of a pentagonal dodecahedron in *Banisteria*, *Rivina*, and, in particular, in a number of Caryophyllaceæ, e.g. *Arenaria*, *Silene* and *Dianthus* (*cf.* fig. 217^{11}). In the Dandelion (*Taraxacum officinale*), and in *Corydalis lutea* many crystalline forms occur, side by side, in the same anther (*cf.* figs. 217^{12} and 218^{4}). The tetrahedron, also, is not infrequently met with. This form occurs in *Thesium*, *Cuphea*, many Proteaceæ and Composites, sometimes with flat, sometimes with curved surfaces (*cf.* fig. 218^{6}). A form, made up as it were of two spherical triangles joined together, occurs in *Circæa* and many other Onagraceæ (fig. 217^{5}).

The above paragraph relates solely to the varieties in form of dry pollen-grains. In the great majority of cases the grains are variously striated and grooved. In ellipsoidal and spherical grains, the grooves run like meridian-lines, so that two poles are distinguishable. The number of the grooves is constant for a given species, and even for whole families of plants. A single furrow is characteristic of the grains of the Tulip-tree, Magnolias, and Water Lilies (fig. 218^{1}), of the Meadow Saffron, Tulip, Lily, Iris, Narcissus, and Snowdrop, of Palms, Grasses, and, indeed, Monocotyledons generally. Two furrows are found on the pollen-grains of *Calycanthus*, several climbing Smilacineæ (*Tamus*, *Dioscorea*), and several species of *Amaryllis*. A very great number of plants have three grooves, *e.g.* Rock-roses, Violets, Poppies, Ranunculaceæ, Roses, Almonds, many Papilionaceæ, Beeches, Oaks, and Willows, Solanaceæ, Gentians, Scrophulariaceæ, and many Composites (*cf.* figs. 217^{13} and 218^{3}). Four grooves have been noticed in several Boragineæ (*Anchusa*, *Nonnea*), some Labiates (*Teucrium montanum*, *Sideritis scordioides*), in *Houstonia*, *Platonia*, *Blackwellia* and *Cedrela odorata*; six in most Labiates (fig. 217^{14}), nine or ten in *Sherardia*, *Borago*, and *Symphytum*; twelve in *Crucianella latifolia*; sixteen in *Polygala chamæbuxus*; twenty-one to twenty-three in *Polygala myrtifolia*. On crystal-like pollen-grains the grooves are extremely delicate, and their number depends on the number of angular ridges.

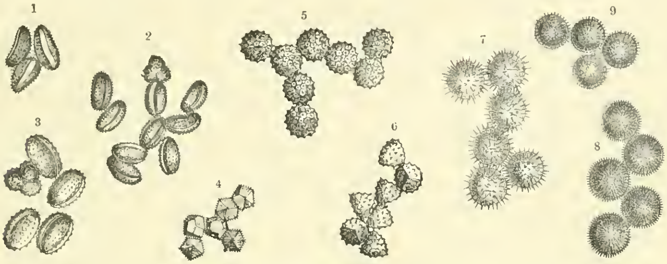


Fig. 218.—Pollen-grains.

^{1} *Nymphæa alba.* ^{2} *Viscum album.* ^{3} *Carlina acaulis.* ^{4} *Taraxacum officinale.* ^{5} *Cirsium nemorale.* ^{6} *Buphthalmum grandiflorum.* ^{7} *Hibiscus ternatus.* ^{8} *Malva rotundifolia.* ^{9} *Campanula persicifolia*; ×200.

A very conspicuous feature of many pollen-grains is the infinitely varied sculpturing, &c., of their walls. Sometimes this takes the form of a delicate dotting of the wall, as in *Asarum*, Meadow Saffron, Rue, Salvia, Gentians, and Euphorbias, many Aroids and Musaceæ (*cf.* figs. 217 [13] and 217 [14]); or the projecting ridges may be transversely striated as in *Saxifraga aizoides*; or, again, delicate striations may run in meridian-like circles (e.g. *Brugmansia arborea*). Sometimes dotted lines are found arranged in various ornamental reticulating patterns. On the smooth surface of the grains of *Thesium alpinum* and *rostratum* reticulations occur, and in the centre of each mesh a distinct dot. Similiarly in Thrift and Sea Lavender (*Armeria* and *Statice*), and in the Corn Cockle (*Agrostemma Githago*). Often the surface presents considerable unevenness. In *Cuphea platycentra* the outer coat is prettily ridged, whilst in many other cases it is finely granulated. The little projecting granules may be either scattered equally over the whole surface, or they may be arranged in networks—which is specially the case in Cruciferæ (*Capsella, Raphanus, Sinapis*). In the Passion Flowers (e.g. *Passiflora Kermesina*, fig. 217 [4]) these networks are inclosed in shallow, ring-like depressions, whilst in *Cobæa scandens* (fig. 217 [1]) the surface has a honey-combed appearance. Sometimes the whole surface is dotted over with little wart-like projections, as in *Centaurea Jacea*, Mistletoe (*Viscum album*), White Water Lily (*Nymphæa alba*), and the tropical Bauhinias (*Bauhinia armata, furcata, cf.* figs. 218 [1] and 218 [2]); or it may be covered with sharp, needle-like prickles, as in the pollen-grains of Composites, Scabiouses, Campanulas, Cucurbitaceæ, Malvaceæ; also in the genera *Armeria, Amaryllis, Canna, Lonicera, Ipomœa*, and *Convolvulus* (*cf.* figs. 218 [3] and 218 [9]).

It is only the superficial layer of the pollen-grain which shows these sculpturings and projections, the inner layer, which abuts immediately upon the protoplasm, is homogeneous. The wall of pollen-grains is, as a rule, three-layered. These three layers are:—the internal one or *intine*, the middle one or *extine*, and the external one or *perine*. The extine and intine arise from the protoplasm of the pollen-cell itself; the perine, on the other hand, is deposited from the matrix in which the young pollen-grains lie embedded. It comes about in this way. The young grains first clothe themselves with delicate walls, which are in due time thickened. This is the extine. Within this they form a second layer, the intine. Lastly, the perine is deposited upon them from without. The intine and extine can generally be readily distinguished as separate layers, but between the extine and perine the boundary is by no means so well marked. The various sculpturings, prickles, and other unevennesses of the outer coat really appertain to the perine.

It sometimes happens at definite spots on the wall of a pollen-grain, from a separation of the molecules there, that little spaces or actual canals arise which open externally by tiny pores. This may be well observed in *Thesium, Prunella, Ipomœa*, and *Gentiana*. In these canals a yellow (rarely colourless) oil is contained, which oozes out in the form of minute drops when the grains are moistened and absorb water. Such at any rate is the behaviour in *Prunella grandiflora* and *Gentiana ciliata*. In many other plants the whole surface of the grain is saturated with this oil. I ascertained that in about 400 out of 520 species investigated by me the outer surface was overlaid with oil. The layer is so thin that with dry pollen-grains it is not visible, but when they are placed in water, the coating is resolved into a number of minute, strongly-refringent droplets, which adhere to the swollen pollen-grains like tiny beads. There is no doubt that this coat consists of a fatty oil, since it is soluble in alcohol and olive-oil, and with osmic acid it turns dark-coloured and becomes congealed.

More rarely are pollen-grains found with masses of a sticky, structureless substance adhering to them. This substance does not form droplets with water, nor does it dissolve in alcohol and olive-oil. It may be termed *Viscin*, from the similarity which it presents to the bird-lime obtained from the berries of the Mistletoe (*Viscum*). Such a viscin is met with on the surface of the pollen-grains of *Fuchsia, Clarkia, Circæa, Gaura, Godetia, Œnothera, Epilobium* — indeed, throughout Onagraceæ and in Azaleas, Rhododendrons, Orchids, and Asclepiads. It is very sticky, and on the slightest touch can be drawn out into delicate threads. The contents of the anthers, as they escape, in the Evening Primrose (*Œnothera*) and Willow-herb (*Epilobium angustifolium*) resemble fringes and tattered ribbons, or a broken net hanging from the adjacent anthers. Under the microscope this substance is seen to consist of pollen-grains, joined together by the sticky strings of viscin (fig. 219^3 and 219^4). The phenomenon is even more striking in the numerous species of *Rhododendron*. In *Rhododendron hirsutum* all the pollen-tetrads of an anther-cavity are held together by a mass of sticky viscin. The anther dehisces by two terminal pores, and from these the pollen-tetrads ooze out to some extent. If the sticky mass be touched with a bristle it adheres, and the whole contents of the anther can be readily withdrawn (fig. 219^1). Its appearance under the microscope is shown in fig. 219^2. In many species, as for instance in the elegant *Rhododendron Chamæcistus* of the Northern Limestone Alps, and in the large-flowered Himalayan

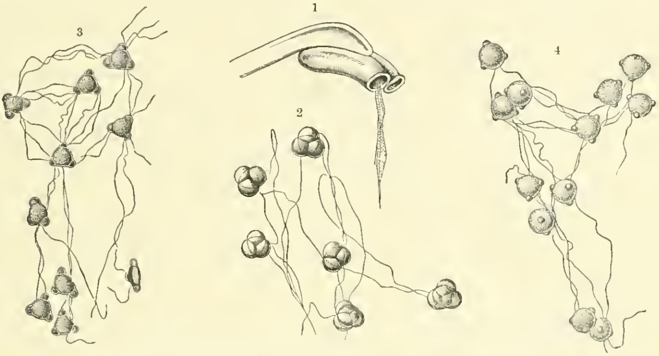


Fig. 219.—Pollen-grains and pollen-tetrads united by threads of viscin.

$^{1,\,2}$ *Rhododendron hirsutum.* ^{3} *Œnothera biennis.* ^{4} *Epilobium angustifolium.* $^1\times 8$; $^{2-4}\times 50$.

species, strings and filaments are woven from the anthers a centimetre long, and insects visiting the flowers touch the strings, stick to them, and carry off with them to another flower generally the whole of the contents of the anther in question. The sticky substance is probably a mucilage formed from the outer wall of the pollen-tetrad, or from the broken-down walls of the mother-cells.

Not to be confused with the little pores communicating with the canals containing the oil are the thin portions of the outer layer, into which the intine projects, cæcum-like, as it swells up in water. It often looks as though the extine were actually perforated at these places; this, however, is not the case, and it is not till later, when the intine pushes through and the pollen-tube is formed, that these places are burst and true apertures arise.

The variety exhibited by these spots is as remarkable as that of the sculpturings. The outmost layer often thins out at those spots where the wall is grooved. As the grain swells up in water, the extine often bursts at the thin region, and may actually peel off (*cf.* fig. 217 [10]). In *Mimulus* and *Thunbergia* the thin region has the form of a spiral, or it may run into loops and convolutions, as shown in 217 [9]. When the intine swells up and bursts the extine, the pollen-grain looks as though it had been pared. In the Passion-Flower the thin places are ring-like, so that with the swelling of the intine, the extine comes away in the form of little lids. The same thing happens in the Gourd, where the lids are very small, and are provided each with a little spine (fig. 217 [3]). A curious condition obtains in *Morina Persica* (allied to the Teasel, *cf.* fig. 217 [2]). Each of the pollen-grains has at its equator three projections, resembling closed bottle-necks with swollen, circular mouths. Very frequently the thin places are disc-like, and may be compared to the glazed port-holes of a ship. It is especially this form which suggests that the outmost layer of the wall is perforated from the beginning. In Umbelliferæ, Rosaceæ, Papilionaceæ, Violets, Rutaceæ, Hypericineæ, Scrophulariaceæ, and other groups of plants, the little circular windows lie hidden in the grooves; in *Cobæa scandens* (217 [1]) they are in the "cells" of the honey-comb, and in Onagraceæ, *e.g.* Enchanter's Nightshade (*Circæa*), the outer coat is continued as a thin investment over the tops of the projecting warts (fig. 217 [5]). The number of windows varies from plant to plant. Cyperaceæ have one; Bromeliaceæ and the Meadow Saffron, Figs and Brugmansias two; Nettles, Oaks, and Beeches, Evening Primroses and Willow-herbs, and many other plants three; Alders and Birches four to six; Currants eight to twelve; Convolvuluses fifteen to eighteen; Carnations, Oraches, and Mezereons twenty to thirty; and Nyctagineæ over thirty.

Having concluded the description of the walls of pollen-grains, the question arises, for what purposes are all these remarkable structures, these grooves and striæ, these chinks and furrows, thorns and spines developed? What is the meaning of the coats of oil and viscin? What of the thin places, and windows, and tiny lids?

Of these the last question is the easiest to answer. As observation shows, pollen-grains swell up with lightning rapidity when they are placed in water. The protoplasm within, destined for fertilization, takes up water from the environment very quickly and energetically. In consequence it swells rapidly, and must have an inclosing wall which will not impede its rapid stretching. For this purpose the thin places and folds are admirably suited. Through them fluids readily pass to the interior, and simultaneously the grooves (previously folded inwards) become inflated, and the pollen-grains come to occupy two to four times the space they previously did. The thicker portions, saturated with oil, play a purely passive rôle in these events. Water cannot enter by these parts, nor do they stretch with the swelling up inside. Later, when the intine has grown out and assumed the form of a tube, the outer wall is not essentially altered. The thin spots have been ruptured, and where lids are present, they are raised; the protoplast, enveloped in the tube-like intine, vacates the extine by one of the thin spots, much as a germinating embryo does its seed-coat. Just as it is of advantage in germination for the seed-coat to be fixed on the substratum, whilst the young plant gets a good hold of the ground, so here it is of value to the young pollen-tube as it quits the extine of the pollen-grain that the coat should be fixed firmly; for this purpose the various ridges, teeth, and spines possess a high significance, serving as a means of anchoring the pollen-grain whilst the pollen-tube is being formed.

But the most important service rendered by the sculpturings and inequalities of the walls consists in the fact that thereby considerable quantities of pollen-grains are enabled to cohere in crumbling masses to the slits of the opened anthers, and to become attached to insects and other animals visiting the flowers for food. Contrasting with this *clinging pollen* is the already-mentioned *dusty pollen*, with smooth and non-adhesive surface. Dusty pollen does not cohere in clusters, nor does it readily attach itself to foreign bodies. On the other hand, the least disturbance or breath of air carries it away in clouds.

It is sufficiently obvious that globular or ellipsoidal pollen-grains with smooth surfaces will be distributed in the form of dust more readily than grains possessing an angular or crystalline form. The former have a smaller surface of contact than the latter. When the surface is, in addition, variously sculptured and raised into folds and inequalities, the points of contact are of course enormously increased· The little projections of the surfaces of adjacent grains interlock like the wheels of a watch; longer ones become entwined like fingers; thus it comes to pass that hundreds of neighbouring pollen-grains hang together like burs. That such masses will readily attach themselves to the hairs, bristles, probosces, and legs of insects hardly needs further demonstration.

This capacity for clinging is much increased when the surfaces of the grains are saturated with oil. The sticky property of the viscin has been already enlarged upon. We may thus summarize the whole matter in the statement that the crystalline forms, the various sculpturings, spines, and other projections, as well as the presence of oil and viscin on the surface are arrangements in virtue of which the adhesiveness of the pollen-grains is increased.

According as one or other of these arrangements is present or absent we find every degree of cohesiveness in pollen—dusty, floury, crumbly, clotted, glutinous, waxy. A marked contrast is noticeable between flowers the anthers of which produce dusty, and those which produce coherent pollen. So pronounced is this, that we shall treat of the pollination of these flowers, and in particular of the transmission of the pollen from flower to flower, under separate headings. Here it need only be added that this distinction between dusty and coherent pollen is found not only with isolated pollen-grains but with tetrads. When the stamens of Heaths (*Erica*) are disturbed the pollen escapes in clouds of dust, just as it does from the catkins of the Hazel. This dust, however, consists, not of isolated pollen-cells, but of tetrads. In Azaleas and Rhododendrons, on the other hand, the pollen-tetrads cling together into sticky filaments, just as do the isolated grains of the Evening Primrose and Willow-herb.

Why it is that the pollen is in some cases in tetrads and in others in isolated grains, why its adhesiveness is promoted by such various means as those enumerated, is difficult to say. These differences are perhaps connected with the varying form of the insect-visitors which carry the pollen away, and of the stigmas upon which it is deposited. That the sculpturings protect the pollen against untimely wetting will be shown in the following chapter.

PROTECTION OF POLLEN.

The approach to Venice from the mainland is by a long embankment, on either side of which the traveller commands an endless vista of marshes full of reeds and rushes broken here and there by expanses of brackish water—the famous lagoons—which themselves exhibit a luxuriant vegetation consisting principally of Pond-weeds and Naiadaceæ. One plant in particular, the Grass-wrack (*Zostera*), is conspicuous for its abundance in the lagoons, covering, as it does, extensive tracts of the sandy mud at the bottom of the shallow water. The leaves are submerged, ribbon-shaped, and of a brownish-green colour somewhat resembling sea-weed, and, when collected and dried, they are known in commerce by the name of "Sea-grass", and are used in the packing of glass, and of late years also for stuffing mattresses and cushions. These Grass-wracks, of which there are two known species, differ so greatly from other Phanerogams, not only in appearance, but also in development and in the mode of pollination, that one might almost be induced to assign to them and their immediate allies a special class, were it not that the fact of the existence of numerous intermediate forms and connecting links tells against their isolation.

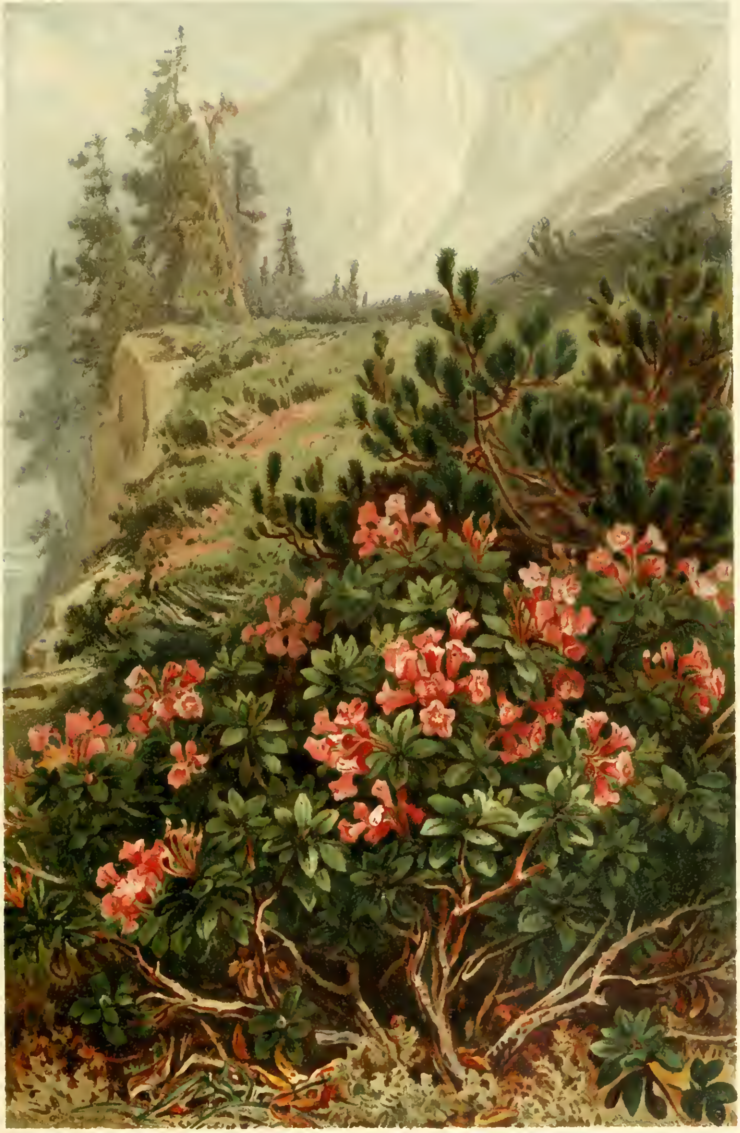
In the first place, the pollen in *Zostera* does not possess the outer coat which is so characteristic of the cell-membranes of most pollen-cells. Further, from the moment the pollen-cells are set free by the opening of the anthers—an event which occurs under water—they exhibit the form of elongated cylindrical tubes. In the plants most nearly related to the Grass-wracks, namely, the genera *Posidonia* and *Cymodocea*, some species of which grow in brackish and some in salt water, the long hypha-like pollen-cells lie in complicated coils and curves within the anther, and when they escape from it, and are carried by the water against the long filiform stigmas they adhere to those structures as do the spermatozoids (spermatia) to the trichogyne in the Red Sea-weeds (*cf.* pp. 60, 61). The filamentous pollen of *Halophila* is even divided by transverse septa into several chambers, or, more accurately, the pollen-cells are aggregated into long strings. The pollen-cells are intercepted under water by the filiform stigmas and grow down them into the ovaries. In the different species of *Naias* as also in those of *Zannichellia* the pollen-cells are spherical or ellipsoidal in shape so long as they are inclosed in the anther, but when the anther opens they assume the form of tubes, and are wafted about by the water until they reach the stigmas. The stigma in *Zannichellia* is triangular and comparatively large, and owing to the fact that three or four such stigmas have their edges in contact, a sort of funnel is formed, which serves to collect the pollen-cells as they float about.

The plants above referred to, about fifty species in all, were classed together by the older botanists under the name of *Naiadeæ*, but are now grouped into the families of the Potamogetonaceæ, Naiadaceæ, and Hydrocharidaceæ. They are all aquatic plants, but it would be erroneous to suppose that all the members of these groups possess the same kind of pollen as is exhibited by the Grass-wracks, and the various species of *Halophila*, *Posidonia*, *Cymodocea*, *Naias*, and *Zannichellia*, that is to say, a filamentous pollen destitute of external coat which is conveyed to its destination by currents of water. On the contrary, thousands of aquatic plants discharge their pollen above the surface of the water and not beneath it. The pollen-cells are spherical or ellipsoidal, have a distinct external coat, and are transported to the stigmas not by flowing water but by the wind or by insects. This is the case even in plants whose leafy parts remain under water throughout their lives. *Aldrovandia*, *Hottonia*, and *Utricularia*, many Pond-weeds (*Potamogeton*) and Water-crowfoots (*Ranunculus*), not to mention many others, always raise their flowers above the surface of the water, so that the pollen may escape into the air and be blown or otherwise conveyed from one flower to another. I have observed that even in the case of the various species of Water-starwort (*Callitriche*), which were formerly said to accomplish their fertilization under water, the anthers open only in the air, and that the staminal filaments grow in length according to circumstances until the anthers project above the surface. If they fail to do so, then the anthers of the flowers in question do not open at all; the spherical pollen remains inclosed and decays, together with the anther and its filament, beneath the water. The far-famed *Vallisneria* (see vol. i. p. 667), too, to which we shall return again later on, only emits the pollen from its anthers into the air. The staminiferous buds, it is true, develop under water; but they detach themselves from the axis of the inflorescence in the form of closed bladders, and do not open until they reach the surface. The stamens then project out of the floating flowers into the air, the anthers burst, and the pollen is set free (*cf.* fig. 227). If the buds are kept submerged artificially, neither they nor the anthers open, but they decay, and the pollen perishes under the water. And, as in the case of these aquatic plants, so also in that of the multitude of plants which germinate and flower on dry land, if the pollen happens to fall into the water or is purposely kept immersed, it is destroyed.

It is thus the fact that the pollen of Phanerogams, with the exception of about fifty species, of which the Grass-wracks may be taken to be the type, is injured by prolonged immersion or subaqueous transport. This obviously suggests an inquiry as to the reason of the hurtful action of water upon cells which require an especial abundance of liquid materials for the development of the pollen-tubes. There is, however, a great difference between the absorption of pure water and the absorption of the liquid substances yielded by stigmas. A pollen-cell deposited upon a stigma gradually takes up the liquids there available, and the pollen-tube pushes out comparatively slowly. If, on the other hand, the pollen-cell is put into water, or is in nature so wetted by rain or dew as to be practically immersed in a water-bath, absorption of water takes place almost instantaneously; the intine is pushed out wherever no resistance is offered by the extine, and in a moment the pollen-cell swells up. Such a process cannot properly be called a development of the pollen-tube. No real growth can take place in so short a time, and what has occurred is simply an expansion of the intine and a smoothing out of the folds which have hitherto lain tucked in. Frequently, indeed, the limits of elasticity are exceeded; the projecting part of the intine bursts, and the spermatoplasm flows out into the water in the form of a finely granulated, slimy mass. In that event the pollen-cell is destroyed, and comes to nothing. But even if the intine does not burst, the pollen undergoes such complete alteration through the rapid absorption of water that its protoplasm loses the power of fertilization. It seems as if the protoplasts inclosed in pollen-cells, subjected to prolonged immersion, were literally drowned. Thus much is certain, that the immense majority of pollen-cells perish under water, and that even if wetted they incur great risk of destruction. This danger, which may be of daily occurrence in case of rain or heavy dew, has to be avoided. In order to preserve the pollen fit for use it must be secured by protective apparatus against the injurious effects of moisture, especially against atmospheric deposits; it must be able to develop under conditions from which this factor—in so far as it is harmful—is, generally speaking, excluded.

In regions where there is a regular alternation of rainy and rainless seasons—in the llanos of Venezuela, the Brazilian campos, the dry districts of India and the Soudan, above all, in the parts of Australia to the south of the tropic where the rainfall is limited to the winter and afterwards ceases for months—the climate itself indirectly affords security to the pollen against risk from water; or, in other words, any apparatus to protect from rain the pollen of plants which flower in rainless seasons would be superfluous. The trees which wave above the grass of the wonderful savannahs of Australia, as also the numerous dry and rigid shrubs which belong to the adjacent "scrub", do not flower until the rainy season is over, when the flowers do not run any risk of being drenched with rain. In the absence of the danger the necessity for any direct means of defence against it also

PLATE V



ALPINE RHODODENDRONS AND MOUNTAIN PINES (TYROL)

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disappears, and in Australia the numerous Mimoseæ and Myrtaceæ and the Proteaceæ, which constitute the principal part of the dense copses just referred to, are accordingly destitute of any contrivance capable of acting as a protection to the pollen. These plants preserve their rigid character even during the flowering season; the filaments bearing the anthers project in large numbers far beyond the small floral envelopes in the Acacias and in the innumerable species of *Callistemon, Melaleuca, Eucalyptus, Calothamnus,* and *Metrosideros,* and the styliform prolongations of the ovaries in Proteaceæ, on the top of which the pollen is deposited when set free from the anthers, spring up and stretch out unprotected far beyond the restricted perianth.

Flowers which inhabit a region where moisture is deposited from the atmosphere in greatest quantity in the flowering season exhibit an entirely different form. In the mountains of Central and Southern Europe, where this coincidence occurs, the plants whilst in flower must be prepared for daily showers. In addition every plant drips with dew in the early morning, and drops of water are deposited on leaves and flowers in the course of the day by the mists as they roll by. It must often happen that the pollen remains for days together hanging to the opened anthers before it is carried away by bees or butterflies to the stigmas of other flowers. Here if anywhere is an instance of the necessity of ample shelter for the pollen. Examine the plants composing the smaller brushwood of such a region, and you will find how great a contrast they afford to the plants of the thickets of Australia. The flowers of the Heather (*Calluna vulgaris*), and of the Bilberry, Bog Whortleberry, and Cowberry (*Vaccinium Myrtillus, V. uliginosum, V. Vitis-Idæa*) have bell- or cup-shaped corollas which hang down from curved stalks with the mouths of the flowers towards the earth, and so cover the pollen-laden anthers. Similarly, we find the Alpine Rhododendrons ("Alpine Roses"), which clothe the mountain sides, with flowers inclined at a right angle to the erect stalks so that the anthers are perfectly sheltered (*cf.* Plate X., after a drawing by E. Heyn).

All the many contrivances whereby pollen is directly protected from wet are of the same nature as the above, the method of protection being by some such roofing in or envelopment of the anthers. That these adaptations should exhibit so much variety in detail in spite of the uniformity of their object is due to the condition that the envelopment must itself not be carried too far. On no account must the dissemination of the pollen or its transport by wind or insects to the stigmas of other flowers be hindered; nay, the very same parts of a flower which shelter the pollen from rain frequently have the additional function of assisting the dispersion of the pollen when the rain is over.

In the enumeration of arrangements for warding off injury to pollen from wetting, the various coverings and protections are described as equally effective for rain as for dew. But this, of course, is not for the same reason. A roof protects structures from rain by intercepting the drops, and from being bedewed since it diminishes radiation from the bodies beneath and thus keeps them at a higher temperature than would otherwise have been the case. This explanation must be borne in mind.

We find, therefore, an amount of variety in the forms of safeguard against wet corresponding to the multiplicity of the adaptations which subserve the purpose of pollen-transport by the wind or by butterflies, bees, beetles, or flies, as the case may be. The means of protection are diversified also according to whether the cover is placed immediately over the pollen or over an entire group of flowers, whether it shelters the newly-opened, pollen-laden anthers or that part of the flower whereon pollen liberated from the anthers is temporarily deposited; and again they vary according as it is the anther-walls, stigmas, petals, involucre, or foliage-leaves which have to serve as roof to the pollen. The Lime-tree affords an instance of the last-mentioned arrangement, its flowers being invariably so placed that at the time when pollen is yielded by the anthers they are covered by the broad, flat foliage-leaves. However sharp the showers to which a Lime-tree is subjected the rain-drops roll off the blades of the leaves, and it is only by exception that any one of the many flowers stationed beneath them is wetted. The same provision is met with in a few species of *Daphne* (e.g. *D. Laureola* and *D. Philippi*), in several Malvaceæ (e.g. *Althæa pallida* and *A. rosea*), and in the *Impatiens Nolitangere*, a plant which possesses other remarkable features and will be the subject of further discussion by and by (*cf.* fig. 220[1]). In *Impatiens* the flower-buds are held by their delicate stalks above the surfaces of the leaves from whose axils they spring, and the leaves are at first folded upwards like erect troughs. Subsequently, when the buds get bigger and their stalks longer, the latter slip down to one side of the leaves and hide beneath them, whilst the leaf-margins still continue to be curved upward. The leaf then flattens itself out and fixes the drooping flower-stalk by means of one of the lobes of its heart-shaped base, and thus indirectly keeps the suspended bud in position, so that when later on the bud and its anthers open, which they do simultaneously, they are roofed over by a smooth lamina, off which the rain-drops roll without ever wetting the flowers or their pollen (fig. 220[1]).

In many Aroideæ the spadix is completely covered by the large sheathing leaf or spathe at the time when the anthers burst, as, for instance, in the curious Japanese *Arisema ringens*, where the spathe curves over the inflorescence like a Phrygian cap, and in *Ariopsis peltata*, where the spadix is protected from rain and dew by a sheathing leaf resembling a boat with the keel uppermost (*cf.* fig. 221[1]). *Genetyllis tulipifera*, a shrub belonging to the Myrtaceæ, bears at the ends of slender, woody twigs inflorescences which at first sight might be taken to be pendent tulips. On closer inspection it appears that the large white leaves with red veins which recall the leaves of the tulip perianth are involucral bracts which cover the closely-crowded flowers and shield them from the rain. Similarly in the case of the Banana and its allies (*Musa, Ravenala*) the flowers are covered over when the pollen is mature by large involucral sheaths which subsequently, after the pollen has been used up and there is no longer any need for protection, detach themselves and drop to the ground. Fig. 220^{2} shows the male flowers of the diœcious Sea-Buckthorn (*Hippophae rhamnoides*), which are arranged in spikes and are seated in the axils of scaly bracts at the bases of the young lateral shoots. In each flower are four anthers which discharge their abundant powdery pollen whilst the flower is still closed like a bud and has the appearance of a little bladder (fig. 220^{3}). This pollen is of an orange colour, and drops to the bottom of the flower, where it remains (figs. 220^{4} and 220^{5}) awaiting a dry wind to transport it to the stigmas of the female flowers growing on other plants often at a considerable distance. Several days may go by before this kind of wind sets in, and meanwhile there is the danger of the store of pollen being soaked by rain or dew and rendered unfit for dispersion. To obviate this risk the pair of curved perianth leaves, which have their concave surfaces turned towards one another, and form, as has been already mentioned, a kind of bladder inclosing the anthers and pollen, dehisce at the sides only. Thus two opposite gaps (figs. 220^{4} and 220^{5}) are produced, whilst at the top the two valves remain joined together and form an arch completely sheltering the mass of fallen pollen from atmospheric deposits. When the needful wind arises it blows the pollen out through the chinks in the bladder and conveys it to the stigmas of other plants of the same species.

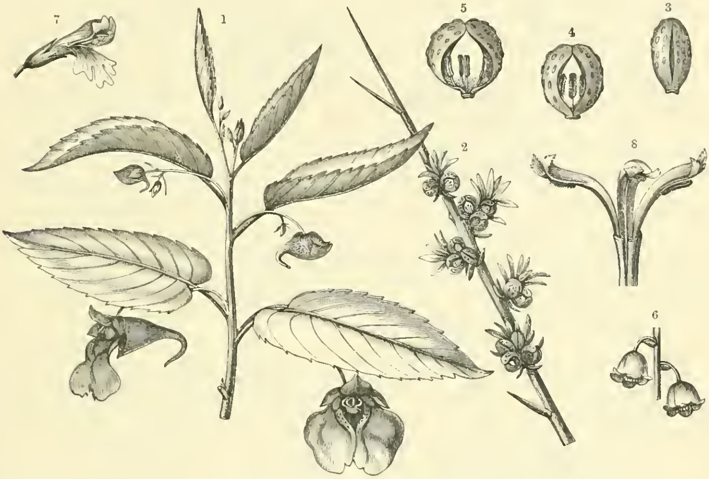


Fig. 220.—Protection of Pollen from Wet.

^{1} *Impatiens Nolitangere.* $^{2-5}$ *Hippophae rhamnoides.* ^{6} *Convallaria majalis.* ^{7} *Euphrasia officinalis.* ^{8} *Iris sibirica.* ^{1}, ^{2}, ^{6}, ^{7}, ^{8} natural size; ^{3}, ^{4}, ^{5} slightly magnified.

Plants of the Globe-flower (*Trollius*) genus, whose species grow in the Arctic regions in damp situations and also further south in mountainous districts of the

Old World, are daily exposed to rain or heavy dew. Nevertheless their pollen is never wetted, the anthers being completely shut in by the perianth-leaves, which are spirally inserted on the receptacle and closely furled one upon another. These flowers have a ring of stalked nectaries round the stamens, and insects which visit them for the sake of the honey are obliged to break through the roof formed by the overlapping perianth-leaves in order to reach the inside of the flower. The pliability of these leaves enables bees by their weight to effect an entrance, whilst falling drops of rain cannot penetrate, but roll off the flower.

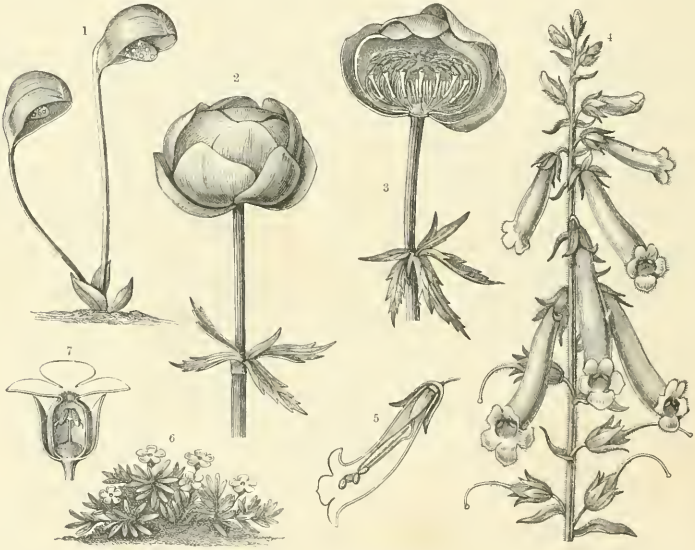


Fig. 221.—Protection of Pollen from Wet.

1 *Ariopsis peltata.* 2 Flower of *Trollius europæus.* 3 The same with some of the floral-leaves removed. 4 *Digitalis lutescens.* 5 A single flower of *Digitalis lutescens* in longitudinal section. 6 *Aretia glacialis.* 7 Single flower of *Aretia glacialis* in longitudinal section (magnified).

Also in Corydalis, Calceolarias, Toad-Flax and Snap-dragon (*Corydalis, Calceolaria, Linaria, Antirrhinum*) the corolla forms a closed envelope round the anthers; and again in papilionaceous flowers the pollen is, up to the moment of an insect's visit, hidden in the cavity formed by the two petals of the keel.

The majority of lipped flowers—Butterwort, Yellow-rattle, Cow-wheat, and Eye-bright (*Pinguicula, Rhinanthus, Melampyrum, Euphrasia, cf.* fig. 220^{7})—as also the Violet (*Viola*), Monkshood (*Aconitum*), and innumerable other plants whose flowers open laterally, do not regularly inclose the pollen, but protect it against rain or dew by means of an arched portion of the flower which forms a roof over it. In *Acanthus* the flowers are inclined laterally, and, though resembling bi-labiate flowers in general appearance, possess no prominent upper lip, the protection of the pollen being effected by a sepal which stretches out at the place where the upper lip would be. A curious arrangement for the protection of pollen by sepals may be observed in the inflorescence of *Hydrangea quercifolia* (fig. 222 [8]), a native of Florida allied to the Hortensias. The flowers of this plant grow in handsome bunches, and are of two kinds: the one kind includes stamens and pistil, but only a very small, greenish perianth incapable of shielding the pollen of the adjoining stamens from rain or dew; the other has neither stamens nor pistil, but has very large, white, expanded sepals which are arranged so as to constitute with their erect stalks a sort of umbrella. The flowers of the latter type are developed on the outermost and uppermost branches of the inflorescence, and are always in a position to stop the rain from falling upon the umbels of small pollen-bearing flowers which are situated underneath them.

In rare cases the stigmas act as pollen-protectors. The most striking instance is that of the genus *Iris*. The stigmas in the Iris are petaloid, and consist of three foliaceous structures gently curved outwards, and each terminating in a pair of dentate apices (*cf.* fig. 220 [8]). The upper surfaces of these foliaceous stigmas are convex and usually somewhat keeled along the middle line, the under surfaces are concave. Beneath each stigma one finds a pollen-laden anther nestling close against the concave surface, and so perfectly concealed that it is impossible that it should ever be reached by a drop of water however heavy the rain.

Flowers of the form called "hypocrateriform" by botanists are adapted to the protection of their pollen on an essentially different principle. The species of *Phlox* and *Daphne* included in this category, the delicate species of Primulaceæ belonging to the genera *Androsace* and *Aretia*, which dwell amid mountain-mists, and the pretty, erect-flowered Primulas (e.g. *Primula farinosa*, *P. denticulata*, *P. Cashmiriana*), all bear flowers which are not roofed in, but have the mouths of their corollas open to the sky, the tubular part of the corolla passing abruptly into an expanded limb (*cf.* figs. 221 [6] and 221 [7]), so that drops of rain or dew collect on the limb surrounding the mouth of the tube. Here it seems inevitable that some drops of water should reach the anthers inserted in the tube. Yet, as a matter of fact, the pollen is kept dry. For, at the place where the tube passes into the limb of the corolla it is abruptly contracted, besides being often also studded with callosities, in consequence of which the opening is so narrowed that, although insects with fine probosces gain access to suck the honey in the flower, any rain-drops that may happen to be lying upon the limb do not gain admission because the air cannot escape from the tube. If flowers of *Aretia glacialis* (fig. 221 [6]), a plant growing on the moraines of glaciers, are examined after a shower, it is found that every one has a drop resting upon it which slightly compresses the air in the narrow tube of the corolla, but cannot reach the pollen upon the anthers lower down the tube. A subsequent shake or puff of wind causes the drops to roll off the limb of the corolla, or else they are got rid of by evaporation; in either case, the flower becomes once more accessible to insects.

In none of the instances hitherto described does any change take place in the relative positions of the foliage-leaves, petals, or petaloid stigmas, whereby the pollen shall be the better protected. On the other hand, there is a long list of plants wherein the protection of the pollen is effected exclusively by means of changes in the position of some one or other of the leaves in question. This occurs especially in all those species which, like the forms last mentioned, have the mouths of their flowers exposed to the incidence of rain, or unshielded, so that radiation is not diminished and dew is formed, but, unlike them, exhibit no sufficient constriction of the tubular part of the corolla to prevent drops of water from falling into the flowers. Such unconstricted, cup-shaped, urceolate, infundibular, or tubular flowers would, if upright, constitute regular rain-collectors, and the water would at once saturate the pollen within the flowers. If flowers of the kind close up temporarily and keep their petals or involucral leaves arched over the interior so long as there is any risk of water collecting there, the requisite security from inundation is attained by very simple means. As a matter of fact, protection of pollen is effected in numerous cases by the closing of flowers. Examples of this are afforded by the flowers of Meadow Saffron, Sternbergias, and Crocuses (*Colchicum, Sternbergia, Crocus, cf.* fig. 223),

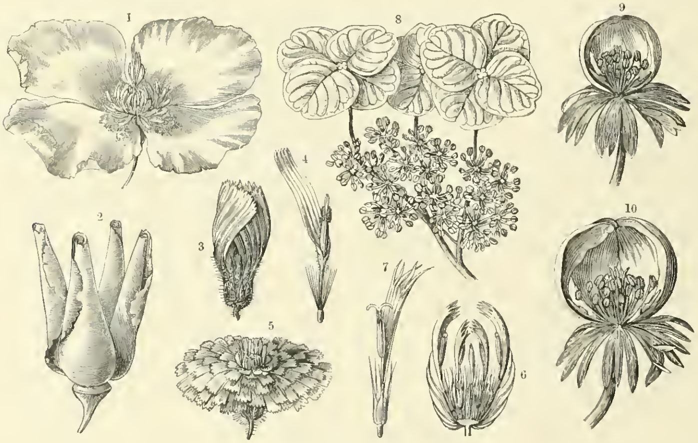


Fig. 222.—Protection of Pollen from Rain.

[1] Flower of *Eschscholtzia Californica* opened in the sunshine. [2] The same closed in wet weather. [3] Floral capitulum of *Hieracium Pilosella*, closed. [4] Single flower of the same plant. [5] Capitulum of the same, open. [6] Longitudinal section through a closed capitulum of *Catananche cœrulea*. [7] Single flower taken from the capitulum in the last stage of flowering. [8] Portion of inflorescence of *Hydrangea quercifolia*. [9] Young closed flower of *Eranthis hiemalis*. [10] Old closed flower of the same.

which lift the cup-shaped limbs of their corollas above the ground in the spring or late autumn, the Gentians of Alpine meadows and their allies of the Centaury genus (*Erythræa*), a host of Bell-flowers with erect blossoms (*Campanula glomerata, C. spicata, C. Trachelium, Specularia Speculum,* &c.), the Peonies, Roses, Flaxes, Opuntias, Mammillarias and Mesembryanthemums, numerous species of the Star of Bethlehem, and Thorn-apple genera (e.g. *Ornithogalum umbellatum, Mandragora vernalis, Datura Stramonium*). The floating flowers of the Water-lily (*Nymphæa*), and the large flowers which are borne on the branches of Magnolias also belong to this group of forms. Throughout the day when the sun is shining the floral cups or funnels of these plants are wide open and often even expanded into stars, whilst swarms of insects hover round them; but at dusk when the dew "falls" the petals close up again and overlap one another so as to form a case (*cf.* fig. 223) upon which any amount of dew may be deposited without affecting the interior of the cup. In damp or rainy weather these flowers do not as a rule open. Thus the period of their being closed coincides with a time when most honey-seeking insects are absent, having either gone to rest for the night, or retired to their hiding-places for shelter from the wet.

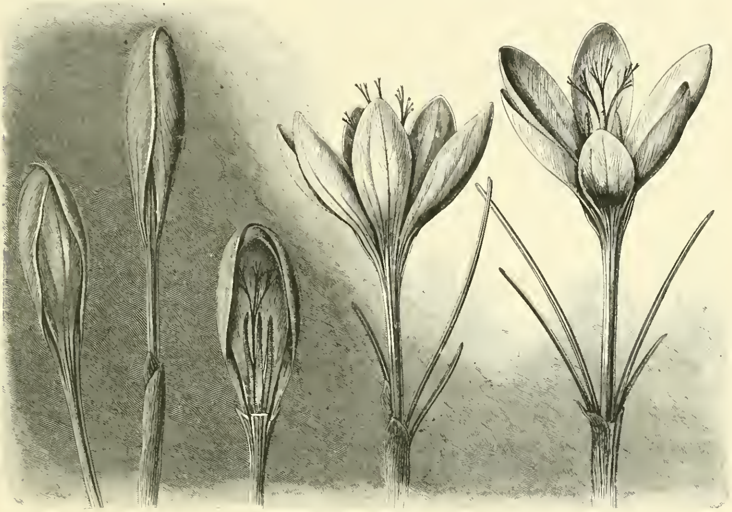


Fig. 223.—Protection of Pollen.

Flowers of *Crocus multifidus.* On the right, flowers open in the sunshine; on the left, flowers closed at night or in wet weather. One of the three closed flowers has some of its perianth-leaves removed.

It is a very interesting phenomenon that petals which close over the anthers in the evening grow much larger in the course of the flowering period. In many species they become double as long as they were at the moment the flower first opened. The enlargement of the petals takes place *pari passu* with certain processes in the development of the anthers to be protected. Some Ranunculaceæ with erect flowers—*e.g.* the Hepatica (*Anemone Hepatica*) and Winter Aconite (*Eranthis*, *cf.* figs. 222[9] and 222[10])—have their pistils surrounded by a crowd of stamens, and these again encircled by concave perianth leaves (petaloid sepals) which are wide open by day but closed at sunset, forming a dome over the stamens. The anthers of these plants do not open simultaneously, but only by degrees. The pollen on the outermost anthers nearest to the sepals is set free first of all, and this happens at a time when the filaments bearing those anthers are still short. It is obvious that comparatively short sepals suffice to shelter these stamens. Gradually, however, the anthers nearer the middle of the flower open; their filaments elongate, and the sepals would now be no longer of sufficient size to form a dome over all the pollen-laden anthers at night time. They accordingly grow in length day by day, until the anthers next to the carpels yield up their pollen. In the case of *Eranthis* the sepals lengthen in this way from 11 to 22 millimetres (*cf.* figs. 222[9] and 222[10]), and in that of *Anemone Hepatica* from 6 to 13 millimetres; that is to say, they actually double their original length.

A curious instance of the closing of petals is that of *Eschscholtzia Californica* (*cf.* figs. 222[1] and 222[2]). By day the four golden-yellow petals are expanded, the pollen falls from the stamens, which grow in a bunch in the middle of the flower, on to the concave petals, and rests on them in a floury layer as much as 1 millimetre in depth. When evening comes the anthers in the centre, having already lost their pollen, are left unprotected, but each petal furls itself up longitudinally in the prettiest manner conceivable, and thus the fallen pollen is sheltered under four little tents.

The flowers composing the capitula of the Dandelion (*Taraxacum*), Lettuce (*Lactuca*), Chicory (*Cichorium*), Nipple-wort (*Lapsana*), and many other Composites, of which we may here select the Mouse-ear Hawkweed (*Hieracium Pilosella* (fig. 222) as type, have tubular bases, but above are produced unilaterally into a strap-shaped structure to which the term ligule is applied. From the bottom of each ligulate flower spring five stamens whose anthers are connate into a tube. This tube is early filled with pollen discharged introrsely, *i.e.* towards the centre of the flower through longitudinal slits in the anthers. The style is embedded in the tube, and as soon as the pollen is liberated it elongates, and, acting like a chimney-sweep's brush, pushes up the pollen which fills the anther-tube until it rests above the opening at the top. The pollen resting on the top of the style is brushed off by insects when they settle upon the capitula. But it is not certain that insects will make their appearance within a few hours of the extrusion of the pollen, and even if they do they only brush lightly over the flowers, and are sure to leave some of the pollen behind, and this pollen is then reserved for another destiny which we shall have to consider more carefully later on. In any case the pollen adherent to the projecting end of the style, near the mouth of the tube composed of the connate anthers, must be protected before nightfall, when there will be condensation of dew, or in case of rain being imminent. This protection is, in fact, afforded to each floret by the ligule of the adjoining corolla, which stretches out laterally and constitutes an umbrella. In the Hawkweeds (*Hieracium*) the ligule bends so as to form a covering over the pollen to be protected (*cf.* figs. 222[3] and 222[5]). In *Catananche*, another Composite, each ligule is spread out flat whilst the sun shines, but in the evening becomes concave and at the same time arches over the pollen belonging to its own flower (fig. 222[6]). We cannot here go into all the differences in detail which occur in connection with this form of adaptation. We must not, however, overlook the fact that in these Composites the ligules of the peripheral florets of a capitulum are always much longer than those of the central florets, and that the pollen of the latter shares therefore the protection from wet afforded by the bending over of the outer ligules. We do not mean to say that the short ligules in the middle of the capitulum are not required to take any part at all in sheltering the pollen. In most instances they, too, stand up and curve over inwards, and act in conjunction with the longer outer ones in preventing the entrance of water. The adaptation of the flowers of *Catananche* is carried so far that the long ligules of the peripheral florets cease to bend inwards when there is no longer any pollen to protect in those florets—that is to say, when the pollen has been brushed off and the florets have entered into their last stage of development (*cf.* fig. 222[7]). The short ligulate florets in the central part of the capitulum must then of course see to the protection of their pollen themselves. This is the reason why one sees only the central ligules of old heads of *Catananche* arched inwards, whilst those near the margin remain motionless and stand out in rays during the dewy night just as they do under the noontide sun.

The mechanism for the protection of the pollen is well worthy of notice in those Composites also in which the central florets of the capitula are all tubular and the peripheral florets all ligulate, and in those where the tubular florets are crowded together on a round disc and encompassed by an involucre of stiff leaves which resemble petals. The Marigold (*Calendula*) may be taken as type of the first group, and the Carline Thistle (*Carlina acaulis*) as type of the second (fig. 224). In these plants the style grows and pushes the pollen out at the top of the tubular florets, just as in the case of the ligulate flowers above described it was pushed up through the hollow cylinder formed by the connate anthers, and above each floret a little lump of pollen is seen resting upon the free end of the style. These tubular florets are, however, incapable of securing their pollen against bad weather, and a division of labour is therefore in some degree instituted within the limits of each capitulum, the ligulate florets or radiating marginal bracts, as the case may be, which produce no pollen, being turned to account for the purpose of sheltering the pollen-bearing florets of the centre. In fine weather the ligulate florets and bracts stand out in rays from the periphery of the capitulum, but in bad weather and at night they are raised and actually bent over the central tubular florets. They are either disposed so as to form together a hollow cone over these florets, or else they overlap one another like the tiles on a roof; often, too, they are twisted together in apparent disorder into a tuft, but they are always so arranged as to afford complete shelter to the central florets and to the pollen exposed by them.

It is a remarkable fact that the length of these incurving rays stands in a definite relation to the diameter of the capitulum. Heads with large discs and great numbers of tubular florets have relatively long marginal rays, those with small discs and few tubular florets have relatively short rays. Moreover, at first when the florets in the middle of the disc are still closed, and only the tubular florets set near the margin have extruded their pollen, the ligulate florets of the ray and the radiating bracts are still short because they only have to shelter their nearest neighbours; but as soon as the flowers in the middle of the disc open, the peripheral florets lengthen so as to be able to cover them also. Thus the roof here actually grows in proportion to the dimensions of the surface requiring shelter.

The changes affecting the position of petals, ligulate florets, and bracts, which have been briefly described and which are classed together under the name of closing movements, take place in most plants in from thirty to fifty minutes, but in a few cases they are much more rapid. Sometimes the process of closing is completed in the course of a few minutes. With Alpine plants it may happen that the flowers shut and open several times within an hour. The warmth imparted by a casual ray of sunshine is sufficient to cause the flowers of *Gentiana nivalis* to spread out their deep-blue petals, but no sooner does the sun disappear behind a cloud than the petals wind themselves round one another in a spiral and close up, forming a hollow cone. If the sun comes out again the corolla is once more open in the course of a few minutes.

In plants with funnel-shaped, tubular, or bowl-shaped corollas, as, for example, the Thorn-apple, Gentians, and the Venus' Looking-Glass (*Datura*, *Gentiana*, *Specularia*), the phenomenon of closing is attended by a complex folding, bending, and twisting of the petals; but as a rule the position assumed by the petals on such occasions is the same as that which they previously exhibited in the bud. Generally speaking, most flowers and heads of flowers when closed at night have the same appearance as they had in the bud state.

For the proximate cause of the movements of closing we must undoubtedly look to alterations in the tension of the layers of tissue involved in the operation. These alterations are due chiefly to variations of heat and light. Fluctuations in the degree of moisture of the air may also partly contribute to the result. In the Carline Thistle (*Carlina acaulis*), indeed, the opening and closing of the heads depends solely on this condition, and temperature is only a factor inasmuch as the relative moisture of the air is generally diminished as the heat increases in the parts of the world where the plant grows. Owing to this property of

Carlina acaulis, its large heads of flowers are used as hygrometers and weather-glasses. When the dry bracts surrounding the tubular florets of the capitulum stand out in rays dry weather and a clear sky are indicated, but when the hygroscopic bracts become erect and subsequently converge, so as to form a hollow cone, wet and cloudy weather is anticipated (*cf.* fig. 224). The significance of these movements of the radiating bracts or involucral leaves to the plant itself is as follows. By day when the air is warm and dry the rays have an outward curve and are spread out widely so as to turn their inner surfaces, which are silvery white, to the sky, and they glisten so brightly in the sunlight that they are visible from a great distance. They thus act as a means of alluring insects to the inconspicuous tubular florets of the disc, and these visitors whilst sucking the honey also load themselves with the exposed pollen and subsequently convey it to other flowers. A large number of humble-bees alight on the open capitula of the Carline Thistle, suck the honey from the florets, and at the same time remove the pollen. If at that moment there were to be a sudden shower of rain the florets of the disc would inevitably be wetted and the pollen ruined. But owing to their hygroscopic sensitiveness the rays rear themselves up on occasion of even a slight increase of moisture in the air such as precedes rain, and, bending inwards, unite into a compact tent, off which the drops of rain roll without being able to do any mischief.

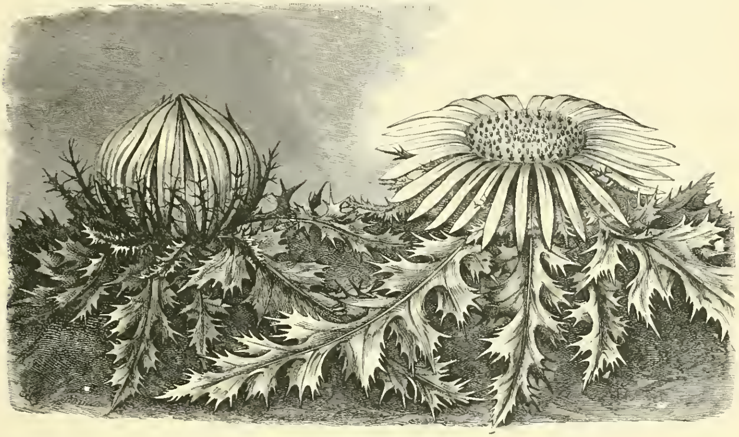


Fig. 224.—Protection of Pollen.

Capitula of the Carline Thistle (*Carlina acaulis*), the one on the right open as in the sunshine, that on the left closed as at night or in bad weather.

Alterations in the form and position of certain tissues of the stamens due to the taking-in and giving-out of water also afford a means of protection for pollen against wet in the case of Plane Trees, and of many Conifers, Yews, and Junipers in particular. The pollen-cases are in these plants borne on squamous or peltate stalks, which are attached to an axis in a manner similar to the scales of a fir-cone. They also possess in common with the scales of a cone the property of closing and bringing their margins into contact when they are moistened, whereas when quite dry they stand away from one another, leaving wide intervening gaps (*cf.* figs. 226 ^{15} and 226 ^{16} with figs. 226 ^{17} and 226 ^{18}). The pollen-dust which is developed in little spherical pollen-cases on the inner faces of the scales, is very liable to be shaken out of these gaping interspaces, but such an occurrence, as will be presently more fully explained, is only advantageous to the plant if dry weather prevails. In damp weather, and especially during rain, such escape would be equivalent to destruction of the pollen. To avoid this risk the gaps close up, an operation which is effected by the scales absorbing moisture and swelling until their edges are in contact, so that the little pollen-cases attached to their inner surfaces are covered up.

In the flowers hitherto described the parts adapted to the protection of the pollen from wind and wet are all leaf-structures or scaly or peltate outgrowths from the connectives of the stamens, and the adapted structure is bent or hollowed out, expanded or folded, as the case may be. Another group of floral forms, scarcely less considerable than the foregoing in point of numbers, secures this protection in a still simpler manner by bendings of the stalks and stem which convert bowl and cup-shaped flowers into pendulous bells. Usually the inflection occurs shortly before the blossoming of the flower, and then the flower retains the drooping position so long as its pollen is in need of protection. Many Campanulas (e.g. *Campanula barbata, C. persicifolia, C. pusilla*), Solanaceæ and Scrophularineæ (e.g. *Atropa, Brugmansia, Cestrum, Physalis, Scopolia, Digitalis*), Primulaceæ and Boragineæ (e.g. *Cortusa, Lysimachia ciliata, Soldanella, Mertensia, Pulmonaria*), Alpine-roses, Winter-greens and Whortleberries (*Rhododendron, Moneses, Vaccinium*), Ranunculaceæ and Dryadeæ (e.g. *Aquilegia, Clematis integrifolia, Geum rivale*), and many Liliaceous plants (e.g. *Fritillaria, Galanthus, Leucojum, Convallaria*) may be seen with their flower-buds supported on erect stalks and turned to the sky so long as they are closed. But before the flower is quite open the stalk curves downward, and the mouth of the flower is thus directed more or less towards the earth. No sooner has the flowering period expired, and with it the necessity for shielding the anthers concealed in the interior of the flower, than the stalks, in most instances (e.g. *Digitalis, Soldanella, Moneses, Fritillaria, Clematis integrifolia, Geum rivale*), straighten out again, and the fruit developed from the flower—especially if a dry fruit—is once more borne at the end of an erect stalk. The phenomenon is illustrated in figs. 221 ^{4} and 221 ^{5}. It is common to hundreds of plants belonging to most widely different families, and exhibits a great variety of modifications. The limits of this work forbid our discussing all these secondary forms of adaptation, which vary partly according to the structure of the stem and flower-stalks, partly according to the form and disposition of the leaves, petals, and stamens. We can only give a brief account of some of the most striking cases.

If the filaments supporting the anthers charged with pollen are small and short, the perianth, which in the inverted flower constitutes their protective cover, is also of small size, as may be seen, for instance, in the case of the Lily of the Valley (*Convallaria majalis, cf.* fig. 220 [6]). A much longer envelope is assigned, on the other hand, to stamens with long filiform filaments. Flowers of the kind possessing large petals but seldom need to be completely pendulous in order to shelter their pollen, it is usually sufficient for them to nod, *i.e.* to droop a little to one side. Thus, for example, the stalks of *Lilium candidum* bend in the flowering season only just enough to incline the mouths of the flowers in a lateral direction. Usually the form of the protective cover is such that the rain can trickle off it in drops. A contrivance far less common is for the petals covering the anthers to form a receptacle out of which the water is periodically emptied. An instance of this is afforded by the South African Sparmannia (*Sparmannia Africana*). The flower-buds are grouped together in umbels, and are borne on stalks, which are curved in a semicircle outwards and downwards away from the main axis, so that the flowers are inverted and their anthers are turned towards the ground and covered over by the petals. When the flower is open, however, the petals are not simply spread out like an umbrella, but are slightly tilted back, *i.e.* upwards. The margins of the petals overlap one another, and their outer surfaces, which, in consequence of the inverted position of the flower are uppermost, thus form a basin open to the sky. When it rains this basin placed above the anthers fills with water, thus adding to the weight borne by the stalk, and as drop after drop increases the strain upon the latter a point is at length reached when the basin tips over, letting the water flow over its edge without wetting the cluster of stamens suspended beneath it. This mechanism preserves the pollen clinging to the dehiscent anthers of *Sparmannia* from rain and dew in spite of their apparent exposure, which to a hasty observer seems to render it inevitable that the stamens should be wetted.

In some plants whose flowers are arranged in racemes a process of inflection takes place before the flowers open, which does not affect the pedicels themselves but the axis from which they spring, the result being that the entire racemes or spikes become pendent. All the flowers are then inverted, and the petals act as a roof in sheltering the pollen adhering to the anthers. This is the case in the Cherry Laurel (*Prunus Laurocerasus*), the Bird Cherry (*Prunus Padus*), the Barberry (*Berberis*), and *Mahonia.* In the Walnut, the Birch, the Hazel, the Alder, and the Poplar (*Juglans, Betula, Corylus, Alnus, Populus*) also, the rachis of the spike changes its position shortly before the dehiscence of the anthers thus providing a shelter for the pollen as it becomes free. The male flowers of these plants whilst in the bud condition are crowded closely together, and form a stiff erect cylindrical spike. But before the flowers open the rachis of the spike grows in length slightly and becomes pendent, whilst the flowers it bears are consequently separated a little from one another and become inverted, so that the floral envelopes, which are composed of little scales and perianth-leaves, are uppermost and the anthers below them (see fig. vol. i. p. 742). Whilst thus suspended beneath the scales the anthers open and the pollen rolls out. It is not, however, immediately blown away, but falls vertically and collects first of all in trough-like depressions which occur on the external surfaces of the separate flowers. Here it remains until there is dry weather and a puff of wind blows it away to the stigmatic flowers, this being accomplished in a manner that will receive closer consideration later on. Up to this moment its resting-place is sheltered from rain and dew by the flowers situated above it on the same spike, and the appendages of each flower thus constitute, on the one hand, a receptacle for the pollen of the higher flowers, and on the other, a roof over the pollen which has fallen upon the grooved backs of the lower flowers, as is shown in the illustration representing the flowers of the Walnut already referred to.

A special interest attaches to those flowers and inflorescences which assume periodically an inverted position and whose stalks possess the faculty of bending, stretching, or turning concomitantly with the alternations of day and night, and of fine and wet weather. Such plants might quite properly be described as weather-cocks. They include forms belonging to most widely different families, but possessing the common attributes—first, that their flowers or inflorescences are borne on comparatively long stalks, and secondly, that they offer their honey and pollen to the flying insects which visit them in shallow cups or flat saucers, or even on plane discs. In the daytime in fine weather when flowers and inflorescences of this kind straighten out and turn their open surfaces towards the sun, they are plentifully visited by such insects as refuse to enter pendent bells and tubes from underneath, and only alight from above on wide, open, and easily accessible flowers, and thus is effected the important function of pollen-dispersion. On the other hand, by becoming pendent at night and in rainy weather—*i.e.* at a time when insects are not commonly on the wing—they ensure security for their pollen and honey against wet. Hence the periodic movement of the axis appears to achieve a double advantage.

In many Campanulaceæ and Geraniaceæ it is the stalks of individual flowers that bend. The widely-distributed species, *Campanula patula* and *Geranium Robertianum* have been selected from the list of those orders for illustration (*cf.* figs. 225 ^{1} and 225 ^{3} with figs. 225 ^{2} and 225 ^{4}). The same phenomenon occurs in many species of Wood-sorrel, Poppy, Pheasant's Eye, Isopyrum, Crow-foot, Wood Anemone, Cinquefoil, Starwort, Chickweed, Saxifrage, Rock-rose, Anoda, Potato, Pimpernel, Jacob's Ladder, and Tulip (e.g. *Oxalis lasiandra, Papaver alpinum, Adonis vernalis, Isopyrum thalictroides, Ranunculus acris, Anemone nemorosa, Potentilla atrosanguinea, Stellaria graminea, Cerastium chloræfolium, Saxifraga Huetiana, Helianthemum alpestre, Anoda hastata, Solanum tuberosum, Anagallis phœnicea, Polemonium cœruleum, Tulipa sylvestris*). In the Scabious given in the illustration opposite (*Scabiosa lucida*, figs. 225 ^{5} and 225 ^{6}), and in several Composites (*Bellis, Doronicum, Sonchus, Tussilago*, &c.) it is the peduncles bearing the capitula which bend; in many Umbelliferous plants (e.g. *Astrantia* *alpina, A. carniolica,* &c.), it is the stalks of the umbels, and in some Cruciferous plants (e.g. *Draba aizoides, Arabis Turrita, Sisymbrium Thalianum*), the axes of the racemes. The above-mentioned Scabious and Composites exhibit a periodic inversion of the entire inflorescence in consequence of the inflection of the axis, and the radiating ligulate florets set round the margin of the capitulum serve to shelter the pollen of the central florets. Similarly in the Umbellifers named, the involucres of the separate umbels, being comparatively large, act in the same way. The fact is also worth notice that in some Willow-herbs (e.g. *Epilobium hirsutum, E. montanum, E. roseum*), the flower-stalks themselves do not bend, but the long stalk-like inferior ovaries curve downward and straighten out again, periodically causing the flowers, which are of a flat salver shape, to alternate between a pendent and an erect position. The inflection of flower-stalks, or, of their substitutes, the ovaries, ceases as soon as the pollen of the flowers concerned has been removed by one means or another, and a shelter for it is no longer needful. The flower-stalks of *Saxifraga Huetiana* only continue to bend so long as the anthers in the flowers they support are covered with pollen, and the long ovaries of the Willow-herbs mentioned above only curve towards the earth on two successive evenings; the third evening,

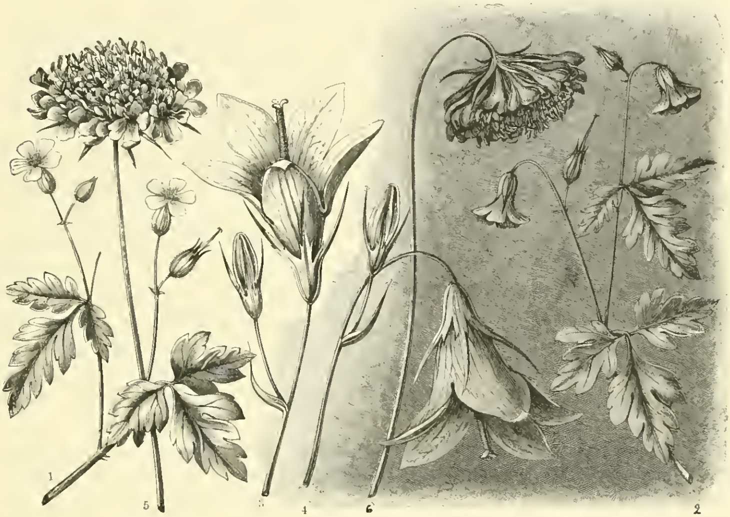


Fig. 225.—Protection of Pollen.

[1] Flowers of the Herb-Robert (*Geranium Robertianum*) in the daytime; the pedicels erect. [2] The same plant with its flowers pendent on curved pedicels, the position assumed during the night and in wet weather. [3] Bell-flower (*Campanula patula*) by day; the flower on erect pedicel. [4] Flower of the same plant inverted for the night or for wet weather, the pedicel being curved. [5] Capitulum of a Scabious (*Scabiosa lucida*) in the daytime; the peduncle erect. [6] Capitulum of the same plant at night or during rain, the peduncle curved and the capitulum inverted.

when there is no longer any pollen to protect from rain and dew, they remain erect.

All these phenomena of inflection and straightening on the part of flowering axes and inferior ovaries are brought about in the same way as the periodic movements of petals and bracts by alterations in the tension of the tissues. These variations of tension are again due partly to vicissitudes in respect of heat and light, and of the degree of moisture of the air. But mechanical stimuli also play an important part, especially such shocks to the flower-bearing axis as are occasioned by the incidence of drops of rain and by gusts of wind. The fact that drops of water are found resting on the nodding or drooping flowers, if the latter are examined before sunrise when there is a heavy dew, or after a shower, tempts one to look upon the inflection merely as a consequence of the strain imposed upon the stalks by the increased weight of the water-laden flowers. No doubt this strain has something to do with the inflection, but it is equally certain that the drooping state does not disappear at once when the water has evaporated and the strain due to its weight has terminated. This persistence of the inflection at all events must be attributed to an alteration in the tension of the tissues of the stem, and no more than the first impulse can be derived from the weight of dew or the impact of drops of rain. Additional evidence of this is afforded by the facts that the process of bending is set up by rain falling on flowers and stem, even when it rolls off immediately, and that pedicels and peduncles also bend over whenever the entire plant is caused to sway about by the wind which precedes a downpour, the stems on these occasions always curving away from the direction of the wind, or, to use a nautical expression, to the lee side.

This phenomenon of the bending of stalks and drooping of flowers before the rain has actually begun looks almost as if the plant had the power of foreboding the approach of bad weather and of adapting itself beforehand in such a manner as to prevent any injury being subsequently inflicted upon it by that destructive agency. Such is the opinion of the peasantry in parts of Europe, and they look upon the inflections above described, as well as the closing of the heads of the Carline Thistle, which was mentioned further back, as a sign of imminent rain. There is, however, as already said, a mechanical explanation of the phenomenon dependent on a change in the tension of the tissues of the stem induced by the oscillations of the plant when subjected to the gusts of wind which usually precede rain, the change of tension being manifested externally by the persistence of the stem's inflection. Moreover, this lasting curvature of the stem may also be produced artificially by inducing the same kind of strain as is caused by the weight of the rain-drops or the vibration caused by rain and wind. If, for instance, you bend the pedicels of various species of *Oxalis* from the erect position they occupy in the middle of the day and hold them down for a time, or if you shake or knock them, the tissues forthwith undergo a change of tension which results in those stalks becoming curved and the flowers drooping towards the ground instead of facing the sky as before. The same is true of the stalk of a Tulip (*Tulipa*), of the long peduncles of *Doronicum*, of the flower-bearing stems of *Asperula arvensis*, *Astrantia major*, *Cardamine pratensis*, *Lychnis flos-jovis*, and *Primula cortusoides*. If you try to straighten the stalks again afterwards you run a risk of breaking them. An interval of some hours elapses before this inflexibility disappears and the tensions existing before the act of mechanical stimulation are re-established and the stems become straight again.

These different changes in the direction and position of petals, bracts, flower-stalks and stems, which take place concomitantly with the alternations of night and day, of storm and calm, cloud and sunshine, often imply a complete transformation in the aspect of the vegetation within a very brief space of time. On warm summer days, when the sky is clear and the air still, the green of the meadows is sprinkled with the colours of innumerable open flowers. The stellate, salver-shaped, and cup-shaped flowers and inflorescences of Anemones, Ranunculuses, Potentillas, Gentians, and Composites are all wide open, so that the upper brightly-coloured surfaces of their flowers are visible from a great distance. Most of them are turned towards the sun, which enhances their brilliancy; several of the flowers and inflorescences—as, for instance, the Rock-rose (*Helianthemum*)—follow the sun, and face the south-east early in the morning, the south at noon, and the south-west in the afternoon. Countless flies, bees, and butterflies swarm and buzz round the flowers in the sunshine. When the sun sets a cool breeze springs up, and there is a copious deposit of dew on leaves and flowers. The insects withdraw to their homes to rest for the night, and the flowers seem to fall asleep too. Petals fold up, heads of flowers close, flowers and inflorescences bend towards the ground and exhibit the inconspicuous outer surfaces of their floral envelopes to the onlooker. Whilst the night lasts the meadow, drenched in dew, continues in a state of torpor, from which it is awakened once more by the warmth imparted by the sun when it rises next morning. A similar change of aspect occurs when a storm is brewing, when the meadow is swept by wind and rain falls upon the flowering plants. In this event also most flowers cover over or wrap up the parts liable to destruction in time to prevent material damage being done to their pollen.

Comparatively few among ordinary meadow plants appear to be in no way affected by these alterations in external conditions. Some seem to be able to dispense altogether with contrivances for protecting their pollen, for when once the flowers have opened the pollen-cases are left free and uncovered even on occasion of heavy showers. Thus, for example, in *Plantago* and *Globularia* the anthers are borne on long filaments and project in both good and bad weather out of the small flowers, which grow close together in spikes and capitula, and it would seem as though their pollen were exposed to inevitable destruction in case of wet. But closer inspection reveals that even these plants are not destitute of apparatus for the protection of the pollen. To the anthers themselves is due the security enjoyed by the pollen developed from their tissues. For if dewy nights or wet weather occur after dehiscence has taken place and whilst the pollen is exposed at the apertures in the anther-cavities, the latter close up again and encase the pollen once more. The mature pollen is then protected from wet just as effectually as it was during the period of its maturation, for no injurious effect can be exercised by rain or dew through the walls of the anther upon the pollen-cells concealed within. When there is a return of warm, dry weather the anthers open afresh in the same manner as on the occasion of their first dehiscence. Precisely the same processes as were described on pp. 91–93 are repeated. If the anthers are unilocular with transverse dehiscence, like those of *Globularia* and the Lady's Mantle (*Alchemilla*; see figs. $226^{5,6,7,8,9,10}$), the sutures open and shut like lips. If the dehiscence is opercular, as in the Bay Laurel (*Laurus nobilis*; see figs. $226^{11,12,13,14}$), the valves shut down again and force the pollen adherent to them back into the open recesses of the anthers. Lastly, if the dehiscence is longitudinal and the anther-walls open outwards like folding doors and at the same time become revolute, as in *Thesium* and *Bulbocodium* (*cf.* figs. $226^{1,2,3,4}$), the movement is reversed in wet weather, and the two valves close completely together again.

In the Arctic regions and amongst the mountains of Central Europe where copious deposits of moisture occur during the flowering season common to most plants, the number of species possessing anthers which open and shut periodically is not great. Besides those already named, i.e. *Bulbocodium*, *Thesium*, and the *Alchemilla*, only the Plantains (*Plantago*) and Ranunculaceæ, especially those with pendulous anthers (*Thalictrum*), remain to be mentioned as exhibiting this phenomenon particularly clearly. It appears to be much commoner in warmer parts, especially in sub-tropical and tropical regions; at all events, this periodic opening and closing of the anthers is exhibited to perfection in the following plants:—Cinnamon-trees, the Camphor-tree, the Laurel and Lauraceous plants generally, Araliaceæ and Cycadeæ, the various species of *Ricinus* and *Euphorbia*, *Cistus*, the Vine (*Vitis*), and indeed the majority of Ampelideæ, the Tulip-tree and Magnolias (*Liriodendron*, *Magnolia*), and lastly, amongst Conifers the genus *Cephalotaxus*.

The phenomenon in question is the result of changes in the condition of the air in respect of moisture, and depends upon the contraction and expansion of the hygroscopic cells which we noticed in the last chapter as being developed underneath the epidermis of the anther-walls. As in the case of the movements of the involucral bracts on the capitula of the Carline Thistle, the process is only affected by heat inasmuch as the relative degree of moisture in the air alters with a rise or fall of temperature. Seeing that under ordinary conditions variations of temperature and increase or decrease of humidity are connected with the alternation of day and night, it is clear that a periodicity will also be manifest in the opening and closing of anthers, and that in the evening when the degree of moisture is increased the anthers will close, remain shut throughout the night, and not begin to open again till after sunrise, when the degree of moisture is diminishing.

In cases where both the anthers and the petals of a flower open and close periodically, the corresponding movements are for the most part accomplished simultaneously; but if the cause of the movement is different for petals and anthers it may happen that there is no such unison. For instance, after prolonged rain, the petals of *Bulbocodium* may open under the influence of a warm spell of sunshine, whilst the anthers still remain closed owing to the excessive moisture of the atmosphere.

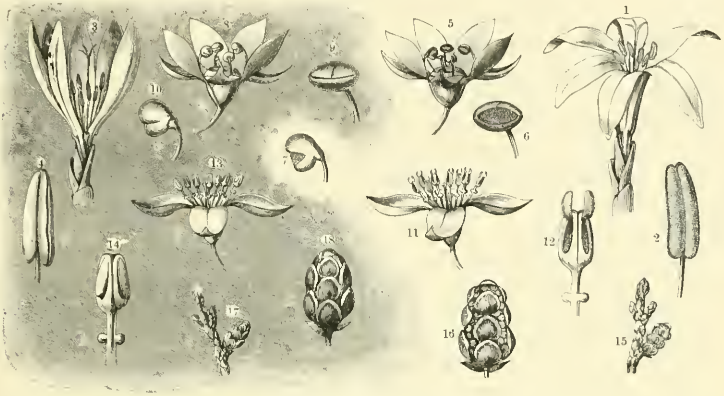


Fig. 226.—Protection of Pollen.

[1] Flower of the *Bulbocodium* with the perianth and the anthers open as they are when the sun is shining and the air dry. [2] An anther from the same. [3] Flower of *Bulbocodium* in moist air; the perianth half open, the anthers closed. [4] An anther from the same. [5] Flower of the Lady's Mantle (*Alchemilla*) with its anthers open in a dry atmosphere. [6], [7] Anthers from the same. [8] Flower of the Lady's Mantle with its anthers closed in rainy weather. [9], [10] Anthers from the same. [11] Flower of the Bay Laurel (*Laurus*) with its anthers open in a dry atmosphere. [12] An anther from the same. [13] Flower of the Bay Laurel with its anthers closed in wet weather. [14] An anther from the same. [15] Staminiferous flowers of *Juniperus Virginiana* in a dry atmosphere. [16] The same magnified. [17] Staminiferous flowers of *Juniperus Virginiana* in wet weather. [18] The same magnified. [1], [3], [15], [17] natural size. The rest × 2 to 8 times.

Anthers close up much more quickly than petals on the approach of danger. They usually take only a few minutes, and in many cases not more than half a minute. The anthers of the Bastard Toad-flax (*Thesium alpinum*) shut up within thirty seconds of their being moistened. In this plant the process of closing is rendered additionally interesting by the fact that the moistening of the anther-walls is effected by peculiar tufts of hairs projecting from the perianth. The briefest possible description of this phenomenon will be given here. The open flower of *Thesium* has the limb of its perianth turned to the sky. This position is maintained unchanged day and night, and even the occurrence of bad weather does not cause any alteration in the direction of the flower-stalks or the position of the flowers. Hence rain-drops falling from above and the dew formed on clear nights must inevitably rest on the open flowers. The immediate wetting of the entire flower is, however, prevented by peculiarities in the form of the limb. The anthers close with great celerity upon the deposition of the drops, the explanation being that the perianth-lobes are connected with the anthers standing in front of them by a bunch of twisted hairs which not only are themselves peculiarly susceptible of being wetted, but conduct the water to the anthers and so cause the anther-walls to close.

A characteristic manner of protecting the pollen by means of the anther-walls after the pollen has been set free, and when it is ready to be carried away by insects, may be observed in several Composites (e.g. *Onopordon, Centaurea*). There is no material difference between these plants and the other Composites discussed on p. 114 in respect of the structure of the tube of syngenesious anthers, the discharge of the pollen into that tube, or the structure of the style and its situation inside the anther-tube; but an essential distinction exists in the fact that the pollen is conveyed to the mouth of the tube not through the elongation of the style but the contraction of the filiform supports of the anther-cylinder. These filaments in *Onopordon* and *Centaurea* contract in response to mechanical stimuli, and in shortening they pull down the anther-tube with them. The top of the style thereupon becomes visible, for the style is sheathed in the tube, and does not shorten when the filaments do so nor change its position. The pollen resting on the style is consequently exposed, and appears in the form of a pulverulent mass on the top of the style surmounting the anthers. If the mechanical stimulation of the filaments is due to the hovering of an insect about the capitulum, the pollen is no sooner exposed than it is brushed off by the insect, and the entire contrivance is obviously so devised that the same insects as cause (by the touch of their legs or probosces) the contraction of the filaments, the retraction of the anther-tube, and the exposure of the pollen may be themselves loaded with the pollen. Up to the moment of the insect's visit, however, the pollen is hidden in the sheath formed by the anthers, and this position is of advantage to it inasmuch as it is there sheltered from rain and dew. The Composites in question have their capitula erect. The capitula of *Onopordon* include neither movable ligulate ray-florets nor radiating bracts capable of closing. *Centaurea* has trumpet-shaped marginal florets, but they do not possess the power of arching over and protecting the tubular florets of the centre. The stalks of the capitula become neither pendent nor nodding in wet weather. In short, the pollen of these particular Composites is destitute of any of the various means of protection which are present in other genera of the same family and which have just been discussed. But instead, the anther-tube itself undertakes the task of sheltering the pollen after the latter is liberated until the moment when the insects which are to carry it away alight upon the flowers.

We need only notice incidentally that extrorse anthers, which turn their recesses filled with coherent masses of pollen towards the earth and their backs to the sky are also to a certain extent protected against wet. A more important provision at all events consists in the fact that the injurious effect of rain or dew on the pollen-cells may be obviated by certain special sculpturings on the surfaces of these cells. Reference has already been made to such cases at the conclusion of the last chapter. They are on the whole rare, and are limited apparently to plants of the tropical and sub-tropical regions. The pollen of the beautiful climbing *Cobæa scandens* (*cf.* fig. 217[1]), one of the Polemoniaceæ, will serve as an example. On the surface of this pollen may be observed a number of little pits with angular rims which make it look at first sight almost like a honey-comb. The pits are not, it is true, so deep as those of a honey-comb, but they are deep enough to prevent the air with which they are filled from being displaced by water dropping upon the pollen. Thus air remains in the pits and thereby affords protection from wet, for it forms an intermediate layer separating the thin parts of the cell-membrane from the water. The thick layers of the cell-membrane which project in ridges are still liable to be wetted, but water cannot penetrate at once through them into the interior of the cell, and such an entrance it is that constitutes the greatest danger to the pollen. A gradual absorption of watery liquid—especially that which is derived from the cells of the stigma—is not only not avoided, but is even necessary for the subsequent development of the pollen-cells.

The instances chosen hitherto for the exemplification of the numerous contrivances whereby the pollen in flowers is protected against wet belong, for the most part, to the category of those which have developed one form of protective apparatus only. Frequently, however, two or even three methods of defence co-exist, so that in case one contrivance should fail there is another in reserve. This occurs in cases where the plant has only a meagre stock of pollen, where the number of flowers on one individual and the quantity of pollen-cells produced from each flower are small, and therefore there is not much pollen to waste, where the time allotted to a plant in which to unfold all its flowers is extremely limited, and where the transport of the pollen from flower to flower is accomplished exclusively by flying insects, whose visits are sometimes delayed for several days when the weather is unfavourable. To mention a few instances with more than one means of protection, in many Anemones and Crow-foots, the Hepatica, the Rock-rose, and the Wood-sorrel (*Anemone, Ranunculus, Hepatica, Helianthemum, Oxalis*), not only do the petals close over the pollen-laden anthers, but the flower-stalks also bend, causing the flowers to nod. In the Daisy (*Bellis*), the Corn Sow-thistle (*Sonchus arvensis*) and many other Composites not only do the ligulate florets of the ray incline towards one another and form a roof over the pollen of the central florets in cloudy weather and in the evening, but in addition the peduncles become bent or pendent. In *Podophyllum peltatum* the pollen is sheltered by the bell-shaped flower, but in addition to this the peltate foliage-leaves are also spread out over the flowers and act as umbrellas. The synchronous closing of both anthers and petals over the pollen when rain threatens is a phenomenon that may be easily observed in a number of plants, as, for instance, in *Bulbocodium* (*cf.* figs. 226[1, 2, 3, 4.]).

The fact is also worthy of note that identical means of protection have not always been evolved by members of the same family of plants. One has one method of defence, another another. This diversity is exhibited particularly by the various genera of Solanaceæ, and by the multifarious species of the genus *Campanula*. In the Solanaceæ we find the following variety of contrivances according to the genus. The flowers of the Potato (*Solanum tuberosum*) fold up in the afternoon and assume an inverted position owing to the curvature of their stalks for the night, but only maintain it whilst the night lasts. The next morning the flower-stalks straighten, and the flowers unfold again. The Deadly Night-shade (*Atropa Belladonna*) has its flowers inverted during the whole of the flowering season, and it is therefore not necessary for the corollas to open and shut. The flowers of the Mandrake (*Mandragora vernalis*) remain erect, but in the night and in rainy weather the tips of the upright corolla-lobes close over the pollen-covered anthers inside. As regards the different Bell-flowers (*Campanula*), those which have very long peduncles—e.g. *Campanula carpathica* and *Campanula patula* (*cf.* figs. 225^3 and 225^4)—are only pendent in the night and in bad weather; by day and in fine weather they are erect. They exhibit pronounced periodic movements resulting in the curvature of their axes. In other Bell-flowers with shorter stalks—e.g. *Campanula persicifolia, C. pusilla, C. rotundifolia*—the buds nod before they open and continue in this position throughout the time of flowering, whilst in those species wherein the flowers are crowded together in heads and have very short stalks—e.g. *Campanula Cervicaria, C. glomerata, C. spicata*—there is in general no curvature of the axes, but the flowers remain upright and guard themselves against rain by means of an inflection of the points of the corolla towards one another which closes the mouth of the bell. Lastly, in the Venus' Looking-Glass, a plant nearly related to the Bell-flowers, the flower closes by means of deep folds formed in the corolla.

When contrivances have to be described which subserve several purposes at the same time, it would lead to confusion to attempt to say everything that there is to be said about them in one place. In such cases it is much more to the purpose to keep one object alone in view even at the risk of appearing one-sided to a hasty reader. This remark is particularly applicable to the means of protection just described as being adopted by plants to preserve their pollen from wet; for there is no question but that most of these contrivances are capable of rendering other services to the plants in question besides the one specified. In many cases the closing of petals effects not only the protection of the pollen, but also its transference to neighbouring stigmas in the event of a dearth of insect-visitors, as will be explained in a subsequent chapter. If a flower-cup filled at the bottom with honey remained open to the rain the honey would be immediately spoilt and would no longer act as an allurement to insects. Hence we may infer that the shutting of the entrance to the interior of the flower, the construction of the corolla-tube, and the change to a nodding position in the case of melliferous flowers preserve not only the pollen, but also the honey from being spoilt by the wet. The narrowing of the corolla-tube and the barricading or complete closing of the entrance to the flower also serve, on the other hand, to keep out certain honey-seeking creatures whose visits would not be advantageous to the plant. Finally, these same contrivances may ward off also such insects as would remove the pollen without conveying the least particle of it to other flowers. In connection with this last function there exist, no doubt, special adaptations besides, one of the most striking of which occurs in the Monkey Flower (*Mimulus*) and in the Hemp-Nettle (*Galeopsis*), and is shown in the illustration of a stamen of *Galeopsis angustifolia* (fig. 216 [19], p. 91). In this instance the anthers are furnished with two lids which can only be opened by a certain proportion of the insects visiting the flowers. Insects with bodies of such a size that when they enter the flower they rub the pollen from the anthers on to their backs are able to lift the lids of the anthers by brushing against them, and they thus expose the pollen. On the other hand, smaller animals which would not load their backs with pollen on visiting the flowers in question or would not convey it to the stigmas of other flowers are not strong enough to open the anthers. Thus the pollen is effectively protected by means of these lids against the detrimental action of small-sized plunderers.

DISPERSION OF POLLEN BY THE WIND.

At the beginning of the last chapter it was stated that the medium wherein the transport of the pollen to the stigmas takes place is, in the great majority of Phanerogams, the air. For the conveyance of pollen between flowers situated at a distance from one another there exist two main agents, viz. the wind and insects. Hence Phanerogams have been distinguished by botanists into "anemophilous" or wind-fertilized, and "entomophilous" or insect-fertilized plants. But these terms, which are adopted in most works on Botany, can only be used in a strictly limited sense. It is no doubt true that there are plants in which the transference of the pollen to the stigmas is effected exclusively by the wind, and others in which the equivalent process takes place solely through the intervention of animals; but, on the other hand, it has been ascertained in the case of a large number of plants that whereas shortly after the flowers open small creatures carry off the pollen and convey it to other flowers, later on, when the flowering period is drawing to a close, the pollen is committed to the wind and by it transferred to the stigmas of neighbouring blossoms. The best instances of this are afforded by several of the Rhinanthaceæ, as, for example, *Bartsia* and the Toothwort (*Lathræa*), and by many Ericaceæ, such as *Calluna vulgaris* and *Erica carnea*, but many more could be mentioned. The conformation of the various parts of these flowers when they first open renders a dispersal of the pollen by the wind impossible; but in fine weather insects visit them in large numbers, and in the act of sucking the honey load themselves with pollen which they afterwards convey to the stigmas of other flowers. Subsequently, however, the conditions are reversed, the supply of honey is exhausted and insects stay away; but, on the other hand, the filaments bearing the anthers have elongated, the pollen-sacs are consequently exserted above the mouth of the corolla, the pollen contained in them is laid bare, and, at the proper time, is blown away by the wind to the stigmas of younger blossoms. Plants of the kind thus appear to have a second contrivance in readiness in case the first fails, so that in any circumstances the object of flowering may be attained. This is indeed a matter of urgent necessity. How easily may it happen that insects are kept away for a long time by unfavourable weather or that they pay but a few visits. Most plants, therefore, take the precaution to provide that under such circumstances the expenditure of energy involved in the production of flowers shall not have been in vain.

It would be inconsistent with the plan of this book to discuss here all the remarkable adaptations which have been evolved for the purpose of providing a supplementary means of dusting the stigmas with pollen in the event of an absence of insects, but it is necessary to make preliminary mention of this one arrangement whereby many flowers, originally entomophilous, subsequently become anemophilous, because it enables us to determine the proper degree of significance to be attached to the division of plants into anemophilous and entomophilous species.

As would naturally be expected, it is, speaking generally, only pollen which is of dusty or floury consistency that is transported by the wind. If it is true, as gardeners assert, that the pollen of Azaleas, which oozes from the anthers in the form of sticky fringes, has on occasion been torn away and conveyed to the stigmas of neighbouring flowers by the wind, the occurrence can only be looked upon as accidental. In ninety-nine cases out of a hundred the viscid strings, if detached by the wind, would not be conveyed to the stigma of another flower, but would adhere to the outside of the calyx and petals, or to the leaves and stem, and would there perish. The same remark applies also to pollen-cells which are bound together into little lumps by oil and viscid substances, or by acicular processes on the outer layer of the cell-membranes. Only in the rarest instances are they carried by the wind to the stigmas of flowers in the vicinity. These are primarily adapted to becoming attached to the bodies of winged insects.

All the more remarkable, therefore, is the fact that in certain water-plants the pollen, though cohering in sticky masses, is blown by the wind on a kind of little boat to the stigmas which are raised above the surface of the water. The phenomenon was first observed in the case of *Vallisneria spiralis*, an aquatic plant which grows in still water, and is widely distributed in Southern Europe. It is, for example, very luxuriant in the ponds, canals, and shallow inlets along the shores of the Lake of Garda, and we will select it as an illustration in the account which follows. The reader is requested first of all to look at the figure on p. 667 of vol. i. It represents a plant living under water with strap-shaped leaves arranged in fascicles at the ends of the creeping stems which are attached to the mud by root-fibres. In the axils of these leaves a variety of buds are produced—in some cases one only which constitutes the starting-point of a new creeping shoot; in others three close together, one of which grows in length parallel to the bottom and develops a foliage-bud at its extremity, whilst the two others grow straight upward, or there may be two, of which one elongates in a horizontal direction, whilst the axis of the other rises towards the surface of the water. Each of the upward-growing shoots terminates in a kind of bladder composed of two concave and somewhat transparent bracts, one of the pair overlapping the other so as to close the bladder securely. Within these bladders are the flowers. Of the individual plants some develop female flowers only, others male flowers only. The former occur singly in the bladders. Each possesses a long cylindrical inferior ovary crowned by three relatively large stigmas with bi-lobed apices and fringed margins. The stigmas are surrounded by an envelope consisting of an upper whorl of three small abortive petals and a lower whorl of three large ovate-lanceolate sepals. These floral segments are invariably so disposed as to allow the finely-fringed margins of the stigmas to project somewhat beyond the perianth-lobes so that pollen may be caught by the fringes from the side. This is also the reason why the three inner perianth-lobes are stunted, for if they were as large as the outer three the stigma would be covered in at the side and no adhesion of pollen could take place. When the stigmas have reached the stage of being adapted to the reception of pollen, the top of the bladder investing the flower splits; the ovary elongates, flower and stigma are pushed up above the envelope, and appear on the surface of the water, where they are spread out in the medium of the air (see fig. 227). The phenomenon described is only rendered possible by the fact that the stalk of the pistilliferous flower lengthens to an extraordinary extent, and does not cease growing until the flower it bears has reached the surface of the water (*cf.* vol. i. p. 667).

The case of the staminal flowers is utterly different. They are not solitary, but grow in large numbers in a bunch on an axis which stands up in the middle of the investing bladder. The two leaves composing the bladder become disjoined under water, and expose the raceme of spherical buds. The buds are still *in situ* on the rachis, which remains quite short, the inflorescence being held at a height of about 5 centimetres above the mud, as is shown in fig. 155, p. 667, vol. i.

Shortly afterwards one of the most wonderful processes exhibited by the vegetable world is gradually accomplished. The flower-buds hitherto connected with the axis of the raceme by diminutive stalks become detached, ascend in the water, and float about on the surface. At first they are still closed and globular, but soon afterwards they open. The three concave leaflets (sepals) forming the outer whorl of the perianth, which have up to that time been arched like cowls over the stamens, are thrown back and assume the appearance of three boats connected together at one spot, and the stamens, which were originally three in number, but of which only a pair are now furnished with anthers whilst the third has remained rudimentary, project obliquely up into the air (see fig. 227). The opening of the petals is immediately followed by the dehiscence of the anthers. The coat of the anther shrivels up rapidly, leaving nothing but a little flap upon which the pollen-cells rest. There are generally only 36 pollen-cells contained in each anther. These are comparatively large and very sticky, they cohere together and form a mass of pollen which is borne upon the thick stamen. Notwithstanding the fact that they are very near the surface of the water, the masses of pollen-cells are not easily wetted. The three sepals underneath them form, as has been said, three boats which respond to the slightest movements of the water without upsetting, and therefore protect their freight from wet to perfection. These little floats are blown hither and thither by the wind and accumulate in the neighbourhood of fixed bodies, especially in their recesses, where they rest like ships in harbour. When the little craft happen to get stranded in the recesses of a female Vallisneria flower they adhere to the tri-lobed stigma, and some of the pollen-cells are sure to be left sticking to the fringes on the margins of the stigmatic surfaces.

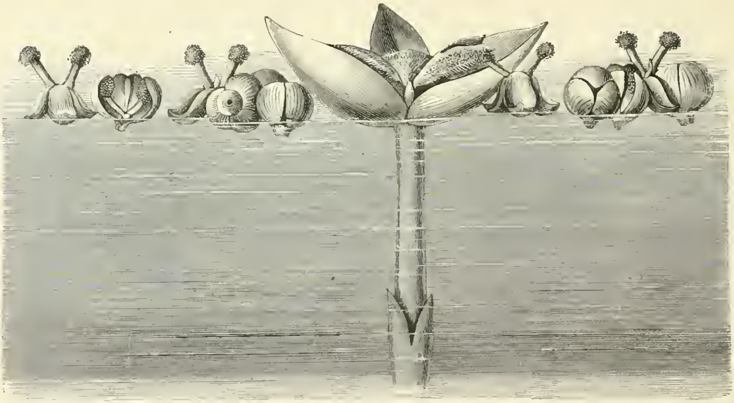


Fig. 227.

Flowers of *Vallisneria spiralis* floating on the surface of water In the middle a female flower with several male flowers on either side of it in various stages of development; some still closed, some in process of opening, some open with their boat-shaped perianth-lobes thrown back. Projecting from the open flowers are the stamens. An open anther is attaching its pollen to the fringed stigmatic margin of the female flower. ×10.

Directly after the adhesion of the pollen, which takes place in the manner shown in fig. 227, the female flower is drawn down under the water. The long flower-stalk assumes a spiral form, and its coils close up so tightly together that the ovary, or young fruit as it now is, is brought to rest at quite a small distance above the muddy bottom of the water.

Up to the present time the conveyance by the wind of adhesive pollen on floats composed of the perianth of the flower is known to exist in the widely-distributed *Vallisneria spiralis*, in *Vallisneria alternifolia*, which is indigenous in tropical Asia, in *Enalus acoroides*, which grows in the Pacific and Indian Oceans, in *Hydrilla verticillata, Elodea Canadensis*, and a few species of the genus *Lagarosiphon*, native at the Cape and in tropical Africa—only 13 species all together, comprised in the little family of Hydrocharidaceæ. This number is almost inappreciable compared with that of the species which produce pollen in the form of fine dust or loose flour, and wherein the pollen is dispersed exclusively and throughout the period of flowering by the wind which blows it away in clouds. It would not be far out to put the number of wind-pollinated plants at 10,000, *i.e.* at about a tenth of the total number of Phanerogams. To this category belong the Conifers, Oaks, Beeches, Hazels, Birches, Alders, Poplars, Walnut-trees, Mulberry-trees, Planes, and the majority of Palms. All these are of the nature of lofty trees, and usually grow in numbers together, each being associated with others of its own kind so as to form extensive woods or plantations, characterized by a close association of individuals. To these must be added the Grasses produced in meadows, prairies, and savannahs; the Sedges, Reeds, and Rushes characteristic of marshes; the Cereals of our fields; Hemp, Hops, Nettles, and Plantains; the common Pondweeds growing in still or running water, and many other plants belonging to families of the most widely different kinds.

One striking characteristic of these exclusively wind-fertilized plants is the absence of fragrant and bright-coloured flowers. The floral-leaves are comparatively small, of a greenish or yellowish colour, and stand out very little, if at all, from the foliage. The interior of the flower is destitute of honey and perfume. It is of no advantage to these flowers to be visited by insects, and accordingly they have no need of any of the means of alluring bees, butterflies, or flies. Hence the absence of odorous substances, of sweet juices, and of brightly-coloured corollas contrasting with the green foliage and visible from afar. We do not mean to say, however, that the flowers of the plants in question are altogether shunned by insects. Many insects covet the pollen itself, and not infrequently they may be seen hovering about the catkins of Hazels and Birches, on the spikes of Plantains, the panicles of Grasses, Rushes, and Reeds, collecting or devouring the pollen. But these visitors play but a very subordinate part in the dispersion of the pollen. By knocking against parts of a flower that are covered with pollen-dust they may, of course, cause some to fall out, but in so doing they only render a service to the plant if the right wind happens to be blowing at the moment and conveys the pollen to the stigmas. If there is no wind, or it blows in a wrong direction, the plants are more likely to be injured than aided by the insects' visits; for, as the stigmas are not brushed by the pollen-seeking insects and therefore receive no deposit of pollen from them, and, on the other hand, the pollen that they shake out is not likely to be carried to the corresponding stigmas if the air is still, it usually happens that anemophilous plants of the kind thus suffer a loss of pollen without obtaining any compensating advantage.

As has been above implied, however, it is not every aërial current that is adapted to serve as an agent for transferring pollen to stigmas. The least favourable winds are those which are combined with atmospheric deposits. Besides the fact that the pollen-dust would be washed away from its resting-places by the rain and carried to the ground, it must perish in consequence of the soaking. Storms of wind without rain are also anything but beneficial, for they forcibly whirl away any pollen that they encounter and carry it in one direction only, and, as but a small proportion, if any, of the stigmas requiring to be fertilized lie in the path of the wind, the greater part of the pollen is wasted.

The result aimed at is best achieved when the pollen-dust, after being removed from the spot where it has been produced or deposited, is distributed uniformly over an ever-extending area, becoming, in a manner of speaking, diluted and forming a cloud of gradually increasing dimensions but diminishing density, so that the thousands of loose pollen-cells which have up to that time been crowded together within the province of the flower and contained in a space about the size of a pin's head are scattered over an area many million times as great. A gradual dispersion of the kind is only occasioned by a gentle wind. The light breezes which sweep through valleys shortly after sunrise, ascending air-currents such as one perceives quivering over heated plains at noon, the alternating land and sea breezes of the coast-winds which, in passing over cornfields, set the corn in gentle waving motion, and in woods cause a scarcely audible rustle—such are the most propitious agents of pollination. It is easy to observe how, at the proper season, under the influence of a gentle wind of the kind one little cloud of dust after another detaches itself from the flowers of the plants in question and slowly soars away. Owing to the fact that the motion of aërial currents is undulatory and undergoes at short intervals alternate augmentation and diminution, the first motion of the pollen as it dissipates itself is also in waves; but the little cloud is soon withdrawn from observation as it proceeds on its way, and the only thing we can clearly discern is that pollen, like dust raised on a road, ascends in an oblique direction.

The form and distribution of the stigmas to be covered with dust-pollen are also in harmony with these conditions. Most plants, whose pollen is in the form of dust, and transported entirely by currents of air, have diœcious or monœcious flowers, and those which develop hermaphrodite flowers exhibit complete dichogamy, that is to say, the andrœcium and gynœcium ripen at different times, so that when mature pollen is being discharged from the anthers of a flower the stigmas of the same flower are already withered, and therefore no longer in a condition to receive the pollen-cells, or else they are still so immature that they cannot be covered with pollen. Any possibility of the transference of pollen from the anthers to the stigmas situated close to them in the same flower being attended with success is as effectually excluded in dichogamous plants as it is in monœcious and diœcious species, and the pollen has to be blown to other flowers in the neighbourhood whose stigmas happen to be in the receptive stage of development. In all these dichogamous plants the flowers with stigmas in the receptive condition are situated higher than the anthers from which mature pollen is being committed to the wind. If you look at any of the species of Plantain (*Plantago*) a few days after they have begun to flower, you find that only the styles with their stigmas ready to receive the pollen project from the uppermost flowers in each spike, whilst the flowers from which pollen is being shaken by the wind occupy the lower parts of the spike.

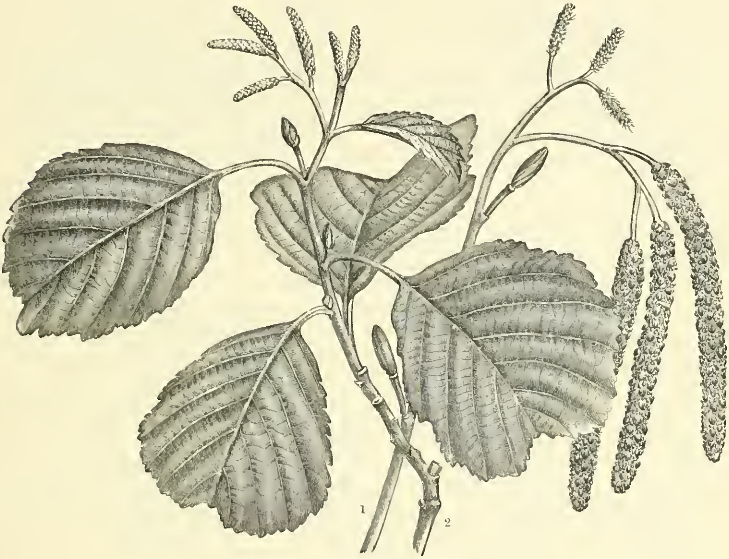


Fig. 228.—The common Alder (*Alnus glutinosa*).

Branch with flowers that open before the leaves are unfolded; the male flowers grouped in the form of pendent catkins, and above them the female flowers grouped in the form of little spikes. [2] Leafy branch at the top of which are the rudimentary inflorescences for the following spring.

In these lower flowers the stigmas are already withered, in the upper ones the anthers are still closed. Therefore, in order to reach the receptive stigmas, the pollen must travel upwards. The same conditions are found in most species of Sorrel (*Rumex*), in the Wall-Pellitory (*Parietaria*), in Saltwort (*Salsola*), in Arrow-grass (*Triglochin*), and in Pondweeds (*Potamogeton*), and many other plants with hermaphrodite but perfectly dichogamous flowers (*cf.* figs. 236 and 237).

This phenomenon is still more strikingly exhibited by monœcious plants, *i.e.* where male and female flowers occur on the same individual. In the Oak, the Beech, the Alder, &c., the catkins of mature polliniferous flowers hang down from the branches in the form of swinging tassels whilst the flowers containing mature stigmas are always above them, whether situated on the same or on adjoining branches (*cf.* fig. 228). In Fir-trees, only the pendent lateral branches of the boughs bear the male inflorescences, which at a distance look almost like red mountain-strawberries, whilst the female inflorescences stand up in the form of little cones on the top of the same boughs like tapers on a Christmas-tree; indeed, many Fir-trees bear the female flowers only on the highest branches close to the summit, and on the lower boughs none but male flowers, and under such circumstances pollen could not possibly reach the stigmas if it were only carried by the wind in a horizontal direction. Even in diœcious plants (*i.e.* where the male and female flowers are on distinct individuals) this relatively inferior situation of the staminal flowers is often to be observed, the end being attained by the fact that the individuals bearing male flowers grow less high than those bearing female flowers. Thus, for example, in Hemp-fields one may see that the plants discharging pollen never reach the same height as those whose flowers are to receive the pollen. Exceptions to the rule do, it is true, appear to exist in the Bulrush (*Typha*), the Bur-reed (*Sparganium*), and many species of Sedge (*Carex*), which possess monœcious flowers, inasmuch as in them the male flowers are situated above the female; but in consequence of the non-simultaneous elongation of the axis, it usually comes about that the mature female flowers of a plant whose stem is amongst the older and taller ones rests at a higher level than the male flowers of the individual next to it whose stem is younger and shorter, and it is easy to convince one's self by observation that here also the pollen is not conveyed by the wind in a horizontal direction but obliquely upwards, and is wafted to the stigmas of neighbouring plants.

This must not, of course, be looked upon as implying that when pollen is dispersed by the wind none descends; but it is unquestionably true in the majority of cases that the clouds of pollen which are carried off by moderate winds at first soar upwards and either reach the stigmas awaiting them at a higher level direct in their way, or else, later on, when the air is still and the pollen-cells are scattered over a wider space, they sink slowly down, leaving a deposit on the stigmas, just as when dust is raised in a room it ends by slowly falling again and covering the furniture with a uniform layer.

In some species at the very moment when the anthers burst open the pollen is ejected violently into the air and ascends obliquely in the form of a little cloud of dust. In this country a good example of this phenomenon is afforded by the Nettles. Anyone standing in front of a bed of Stinging Nettles on a bright summer morning, and waiting until the first rays of sunshine fall on the flowers, will be surprised to see small pale-coloured clouds of dust ascending here and there from amidst the dark foliage. At first the clouds are solitary, and are given off at measurable intervals; by degrees they become more frequent, and at times one may see five or six or more arising at the same moment and at no great distance from one another. But gradually the little explosions become less frequent again, and in another half-hour there is an entire cessation of the phenomenon. On inspection one easily discovers that it depends on the fact that the filaments bearing the anthers are coiled in the bud, and suddenly spring up at the same moment that the dehiscence of the anthers takes place.

The species of the genus *Parietaria* and many tropical Urticaceæ behave in the same manner in this respect as our Nettles. As an instance may be taken *Pilea microphylla* (also known under the name of *Pilea muscosa*), which grows native in Central America, and is often raised in botanic gardens with a view to demonstrating the phenomenon here alluded to. One only has to sprinkle the plant with water at a time when it is covered with flower-buds and then take it out of the shade into the sunshine, and the phenomenon is immediately exhibited. All over the plant the flower-buds explode, and a whitish kind of pollen is discharged into the air in the form of a little cloud. Many Moreæ also display this phenomenon, as, for example, the Paper Mulberry-tree (*Broussonetia papyrifera*), an illustration of whose flowers is given in fig. 229. The male flowers are arranged in spikes (229^{2}), and each flower consists of a sepaloid perianth with four stamens

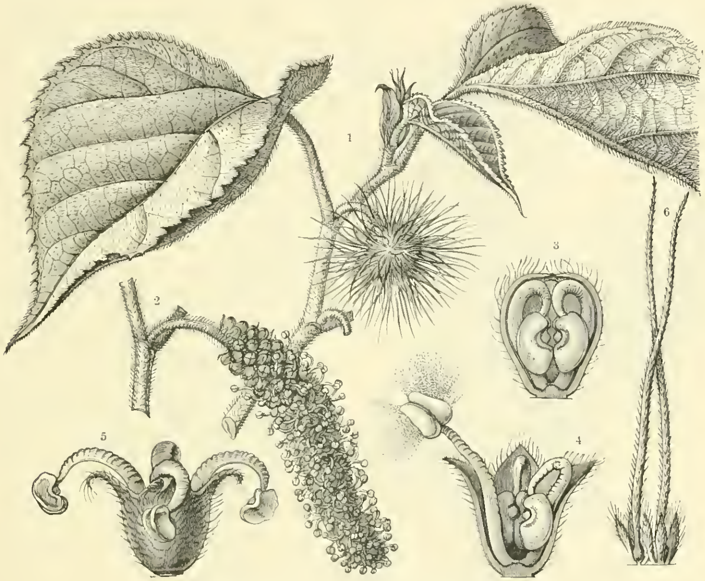


Fig. 229.—The Paper Mulberry-tree (*Broussonetia papyrifera*).

^{1} Leafy branch with capitulum of female flowers. ^{2} Piece of a branch stripped of its foliage with spike of male flowers. ^{3} An unopened male flower in longitudinal section. ^{4} An open male flower in longitudinal section; two of the filaments are still tucked in, one has sprung up and is expelling the pollen from the opened anthers. ^{5} An open male flower with all its stamens already uncoiled and the pollen discharged from the anthers. ^{6} Two female flowers with long hairy stigmas. ^{1}, ^{2} natural size; $^{3-6}$ ×4–5.

upon it. The filaments are very thick and, in the closed bud, are tucked in (229[3]); they are in a state of tension like a spring, but as soon as the cup-shaped perianth opens the filaments spring up one after another, whilst at the same instant the anther-cavities burst open and the pollen is ejected with force into the air (229[4]). When all the anthers are empty the filaments curve backwards (229[5]), and soon afterwards the entire spike of flowers drops off the axis, it being no longer of any value to the plant.

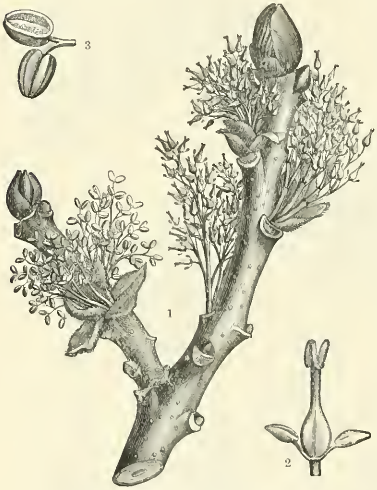


Fig. 230.—The Ash (*Fraxinus excelsior*).

[1] Small bifurcating branch, the left-hand limb of the fork bearing male flowers, the right-hand limb bearing hermaphrodite flowers. [2] Hermaphrodite flower. [3] Two anthers; the upper one open, the lower one still closed. [1] natural size; [2], [3] × 5.

In all these plants ejection of the pollen only ensues when a light, dry wind blows at sunrise and causes an alteration in the tension of the tissues concerned. If there is no wind at all, or the air is close and damp, or if it rains, the opening of the flowers and ejection of the pollen do not take place, or rather they are postponed until the atmosphere has become dry again and a breeze arises which causes the flowering branches to sway about. The results of actual observation are of importance to a proper understanding of the dispersal of pollen-dust. For it thus appears that the air in motion has to start two processes which supplement one another, and must operate in rapid succession if the pollen-dust is to reach the right place and not be lost. The same current of air which causes a liberation and expulsion of the pollen by shaking the flowering axes and by altering the tension of the tissues of the flowers, also carries the pollen away from the spot where it has been produced and conveys it to its destined goal; and this statement applies to the full extent not only to the case of resilient stamens, but also to all other instances of anemophilous pollination where the pollen is in the form of dust.

A similar phenomenon is observed in the case of plants with short, thick filaments and comparatively large anthers filled with pollen of a floury consistency. The *Phillyrea*, the Pistachio-nut (*Pistacia*), the Box-tree (*Buxus*), and most Ashes, especially the common Ash (*Fraxinus excelsior*, see fig. 230), may serve to illustrate this group of plants. The development of the carpels in each flower precedes that of the pollen. At a time when the relatively large fleshy stigmas stretch out far beyond the limits of the inconspicuous floral envelope, and are already capable of taking up the pollen, the anthers may be seen to be still tightly closed (230[1] and 230[2]). The latter do not open till two or three—often even as much as four—days later, and only then in the event of the air being dry. Dehiscence is accomplished by longitudinal fissuring of the anther-lobes. The edges of these fissures contract very speedily, so that each of the pair of anther-lobes is converted into an open recess wherein the pollen lies in the form of a floury or powdery mass (230[3]). Just before dehiscence the anthers place themselves in such a position as to ensure the fissure being turned upwards, so that the recesses full of pollen are not emptied so long as the air is still. It is only when the flowering branches begin to sway to and fro that the pollen falls out of the loculi and is blown away in the form of a cloud of dust by the same breeze as set the boughs in motion.

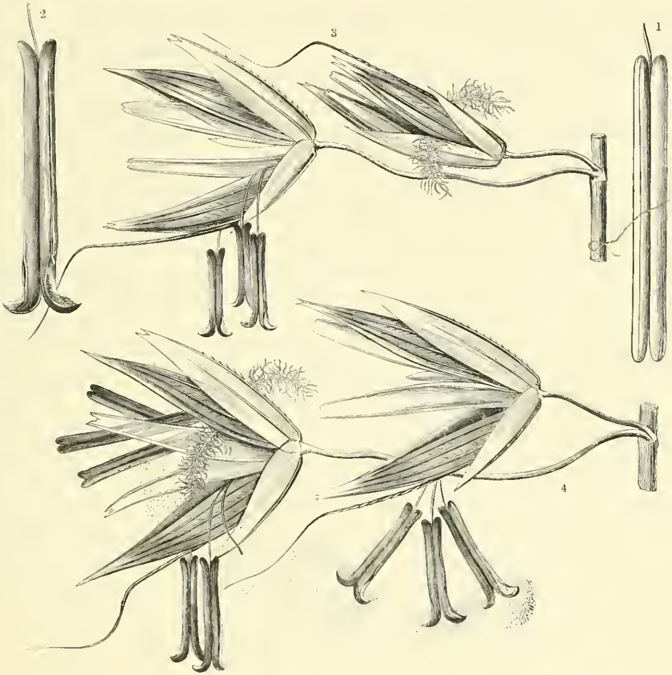


Fig. 231.—*Avena elatior.*

[1] A closed anther. [2] An open anther. [3] Spikelets on a calm day with glumes distended and anthers pendulous. [4] Spikelets in a wind. The pollen escaping from the pendulous anthers in the spikelets to the right; in that to the left (and below) the anthers (two only remaining) have shed their pollen; in a third flower (in the same spikelet as the last-mentioned) the anthers are still closed and in process of being exserted. [1], [2] × 12; [3], [4] × 5.

In another group of plants the anthers are borne on long filaments, and are set oscillating and vibrating by the least breath of wind, the pollen being in consequence discharged in little pinches as though from a sugar-sifter. If the flowers of this kind of plant contain pistils as well as stamens, the relative development of the two sets of organs is always so regulated that the stigmas are already perfect and adapted to the reception of pollen at a time when the anthers of the same flowers are still hidden beneath the floral or involucral envelopes and the pollen is consequently immature. By the time the pollen is completely developed and is in a state to be discharged from the opened anthers, the stigmas of the flower in question are withered and are no longer capable of taking up the pollen. Hence it follows that in these plants the pollen-dust must be transported to other flowers which happen to be at a younger stage of development if fertilization is to be brought about. This is what occurs in nature through the instrumentality of gentle breezes which impose a tremulous motion upon the anthers.

In the first rank of plants belonging to the above category stand the Grasses. Their mode of pollination is so remarkable that it is worth while to look into it a little more closely. One group of Grasses—of which *Avena elatior*, represented in fig. 231, is an excellent example—commences the process under discussion by a sudden distension of the bracts (known by the name of glumes) through the instrumentality of a special turgid tissue situated at their base. The result is that the anthers, till then concealed, are exposed, and it becomes possible for them to be exserted beyond the glumes into the air. This exsertion is effected by an extraordinarily rapid longitudinal growth on the part of the filaments. It has been calculated that in some grasses the filiform filaments elongate to the extent of 1–1·5 mm. in the course of a minute, and that usually in ten minutes they are three or four times as long as they were originally. In one subsection of these plants the filaments grow downwards, in another horizontally, and in a third straight upwards towards the sky. The turgidity of the cells in these delicate filaments is so great as to enable even those which grow vertically upwards to support the weight of the anthers without bending. In the case of those Grasses whose stamens grow downwards from the beginning it does no doubt look as though this direction were assumed in consequence of the weight of the anthers. This is not, however, the fact. A high degree of turgidity exists here also, and if one inverts the inflorescences of this kind of Grass, the stamens which have just completed their longitudinal growth remain quite stiff, in spite of their extreme slenderness, and project straight up. Soon after, it is true, this condition ceases. The filaments become slack; those that were erect nod and droop, those that were horizontal fall down, and the anthers are then all suspended at the ends of oscillating threads.

The dehiscence of the anthers is accomplished synchronously with these changes in the filaments. As long as the anthers lay hidden beneath and protected by the glumes they were straight and linear in form (see fig. 231[1]). Each anther consists of two contiguous parallel lobes, and each lobe has a line running longitudinally down it, along which dehiscence takes place. This operation invariably commences after the anther has assumed a pendent position. The filaments and anthers are joined together by a slender connective, and the tissue of this connective is, as it were, articulated so that the anther is capable of turning freely without becoming detached (a condition termed *versatile*). Hence under any circumstances the requisite position can be assumed; that is to say, the at first uppermost ends of the anthers can be made to hang down whether they are on pendent, or on horizontal, or even on erect filaments. When this inversion has been accomplished the anther-lobes open along the sutural lines already referred to. The slits only gape open for a short distance from that extremity of the anther which is now lowest. This partial opening is in some measure dependent on the further circumstance that at the dehiscent portion the two anther-lobes separate from one another and curve round in opposite directions, as is shown in fig. 231². The significance of this inflection lies in the fact that the powdery pollen is prevented from falling out of the loculi the moment the slits are formed. For the curved ends of the anther-lobes assume the shape of little hollow boats in which the pollen may rest for quite a long time if the air is still (fig. 231³). It is not till a gust of wind sets the anthers swinging that the pollen-dust is blown away in the form of a small cloud (fig. 231⁴, to the right). On the first occasion only the tiny heap pertaining to the dehiscent extremity of the anther is removed, but this is immediately replaced by fresh pollen pouring down from the upper indehiscent portion of the anther. This new supply naturally has no long time to wait, but is blown away by the very next gust. The process may be repeated several times, and generally does not cease until there is no longer any pollen left. When the anthers are quite emptied they drop off the filaments in the form of dry husks. Usually, however, this detachment of the anthers does not take place till several hours after pollination, and in the majority of Grasses, plants which have flowered in the early morning or during the day still have their empty anthers hanging to the spikes or panicles, as the case may be, at sunset.

The changes preceding pollination are much more markedly dependent on the weather in Grasses than in other plants. The temperature and hygroscopic condition of the air in particular play an important part. Rain and low temperatures may delay the splitting asunder of the glumes and the extrusion and dehiscence of the anthers not merely for hours, but for days. A very dry atmosphere accompanied by a high temperature also has the effect of retarding the processes above described. The most favourable conditions for pollination in the case of most Grasses prevail in the early morning at an hour when there is still some dew lying on the meadows, when the first rays of sunshine fall obliquely upon the flowers, and the temperature is rising gently and a light breeze sets the spikes and panicles in motion. Under such external conditions as these the phenomena of flowering and pollination are accomplished with astonishing rapidity. In some Grasses an observer may see the glumes relax and spring open, the stamens grow out, the anthers open and the pollen scattered, all in the space of a few minutes. The earliest discharge of pollen begins between 4 and 5 a.m. in the height of summer, and the plants which take part in it thus early are the Meadow-grass (*Poa*), *Kœleria*, and *Avena elatior*. A little later, between 5 and 6 o'clock, comes the turn of the Quaking-grass (*Briza media*) and *Aira cæspitosa*, and of Wheat and Barley (*Triticum, Hordeum*). Between 6 and 7 pollination occurs in Rye and in a great number of different Grasses which grow in meadows, such as Cock's-foot-grass (*Dactylis*), *Andropogon*, the Brome-grasses (*Brachypodium*), and many species of Fescue (*Festuca*). Between 7 and 8 o'clock the pollen is liberated from Oats of the *Trisetum* group, from the Fox-tail-grass (*Alopecurus*), Timothy Grass (*Phleum*), and the Sweet Vernal Grass (*Anthoxanthum*). An interval now intervenes, at least amongst the indigenous Grasses. Of exotic species which are cultivated in gardens the following discharge their pollen in the course of the forenoon, viz. the Millets (*Panicum milliaceum* and *Sorghum*) between 8 and 9 o'clock; *Setaria Italica* and the Brazilian Pampas-grass (*Gynerium argenteum*) between 9 and 10 o'clock. Towards noon indigenous Grasses come again into play. About 11 o'clock pollination takes place in most species of the Bent-grass genus (*Agrostis*), and between 12 and 1 in Melic-grass (*Melica*), *Molinia*, Mat-grass (*Nardus*), *Elymus*, *Sclerochloa*, and several species of *Calamagrostis*. In the course of the afternoon the process takes place in a few isolated species, as, for instance, in some Brome-grasses at 2 o'clock, in a few species of Oat (*Avena*) at 3, in *Agropyrum* at 4, and in *Aira flexuosa* between 5 and 6. It is worthy of note that the Soft-grass (*Holcus*), under favourable atmospheric conditions, opens its glumes, pushes forth its anthers, and liberates pollen twice a day, once in the morning at about 6 o'clock, and a second time in the evening at about 7—provided always that the temperature of the air is not less than 14° C. The entire process lasts in most cases from 15 to 20 minutes for each flower.

With the opening back of the glumes and extrusion of the anthers are often connected alterations also in the position and inclination of the stalks which bear the spikelets. For example, the pedicels of the spikelets of *Agrostis*, *Apera*, *Calamagrostis*, *Kœleria*, and *Trisetum* divaricate from the axis, so as to form with it angles of from 45° to 80° for the period of pollination. But as soon as the pollen is discharged all these stalks move back towards the main axis of the inflorescence, and the panicle, as it were, contracts. These movements are obviously designed to give sufficient room to the anthers when they are exserted, in order that they may oscillate freely and so disperse their pollen. In those Grasses where the flowers are crowded together in close spikes, and also in the large *Carex* section of the Cyperaceæ, the bracts do not spring open but only relax, and sometimes merely to such a slight extent that it is scarcely noticeable on cursory inspection. The thread-like filaments are also only partially visible in cases of the kind, the anthers are pushed forward and raised above the glumes through the rapid growth of their filaments. As soon as a filament reaches the proper length its upper extremity becomes pendulous, and the anther hangs from it and encounters no obstacle to movements such as are required to shake out the pollen.

As in the case of Grasses and Sedges, so also in Hemp and Hops (*Cannabis, Humulus*), and in numerous species of Sorrel and Meadow-rue (*e.g. Rumex alpinus* and *R. scutatus, Thalictrum alpinum, T. fœtidum, T. minus*) the pollen-dust is shaken out of anthers which are pendulous at the ends of delicate filaments; only, in these plants not glumes but small perianth-leaves form the protective envelope round the anthers before they open. Moreover, in Hemp and Hops, and the above-mentioned species of Meadow-rue, the anther-lobes do not burst wide open when they dehisce, but exhibit parallel slits which are at first so narrow that the pollen can only shake out little by little. Plantains (*Plantago*) also have their pollen shaken out of the anthers, which are borne on long filaments, by the wind. The filaments are tucked in so long as the flower is in bud, but when the petals unfold the filaments straighten out and project beyond the floral spike. The versatile

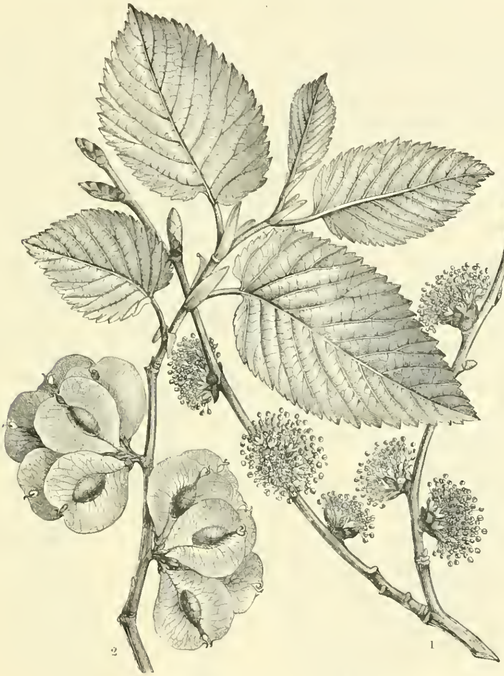


Fig. 232.—The Elm (*Ulmus campestris*).

¹ With flowers. ² With fruits.

anthers borne by these filaments are broad and for the most part heart-shaped; the two lobes of which each anther is composed only open on the side turned to the sky, so that the small gaping slit through which the pollen has to be discharged into the air faces upward. Consistently with this fact we find that in Plantains it takes a couple of days to disperse all the pollen. The same category includes the Elms

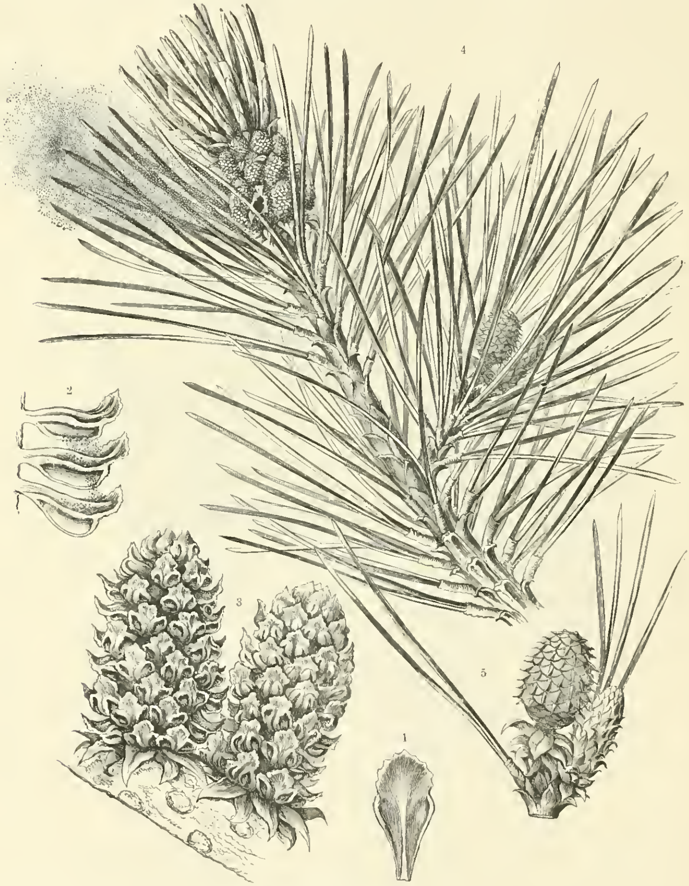


Fig. 233.—Mountain Pine (*Pinus Pumilio*).

[1] A single polliniferous scale (stamen) seen from above. [2] Three polliniferous scales, one above the other, seen from the side. The pollen falling from each anther alights on the upper surface of the stamen next below. [3] Two spikes of polliniferous scales. [4] Branch with apical group of staminal flowers from which pollen is being discharged. [5] Female flower. [1], [2] ×10; [3] ×8; [5] ×2; [4] natural size.

(*Ulmus*, see fig. 232), the Japanese Bocconia (*Bocconia Japonica*), the Meadow-rues with erect and divergent stamens (*Thalictrum aquilegifolium*, *T. angustifolium*, *T. flavum*, &c.) and several species of *Poterium* and *Sanguisorba*. The filaments of Elms are straight at all times, but they elongate shortly before the anthers open to about double their original length, and the dehiscent anthers are then displayed as pairs of gaping valves. In *Bocconia* the anther-cavities are in the form of long narrow niches, and the erect, radiating, filiform filaments vibrate under the slightest breath of wind like the aigrettes ladies sometimes wear on their heads. In the species of Meadow-rue which grows commonly over the lower Alps (*Thalictrum aquilegifolium*), and in the Siberian Burnet (*Sanguisorba alpina*), the stamens are clavately thickened towards the top, and are organized like those of Bocconia in such a manner as to be easily set swinging even when the air is only slightly stirring. The various species of *Plantago*, *Thalictrum*, and *Ulmus* are also remarkable for the fact that the fissures formed in their anther-lobes during dry weather close up quickly in the event of rain, and remain shut until the rain has ceased and the atmosphere has again become dry.

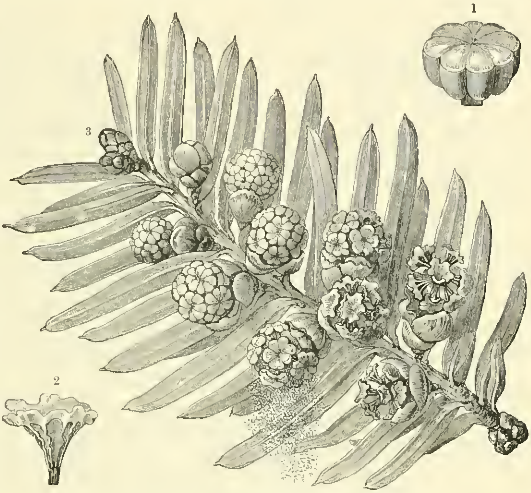


Fig. 234.—Male Flowers of Yew (*Taxus baccata*).

[1] Anther with closed pollen-sacs. [2] Anther with its pollen-sacs open and empty. [3] Branch whose lower flowers are discharging their pollen. [1], [2] × 2; [3] × 7.

In all the cases discussed hitherto the pollen escapes from the place where it originates into the air direct. But there are also a large number of plants whose pollen falls in the first instance on to some spot within the province of the flowers, where it is protected from becoming wet, and in which it remains for a period of varying duration; nor is it blown away until conditions favourable to its dispersal obtain in the environment. Very different parts of a flower are utilized in this manner as temporary halting-places for the pollen. In Pines and Firs the backs of polliniferous scales subserve this purpose in a curious way. The upper surface of each anther-scale in the Mountain or Dwarf Pine (*Pinus Pumilio*) is slightly excavated owing to the lateral edges being reflexed and the broad membranous scale in which the connective terminates being turned up, whilst on either side of the middle line there is a shallow trough (fig. 233 [1]). It is easy to convince one's self of the fact that these excavations serve for the reception of the pollen which falls from the anthers above them (see fig. 233 [2]), and inasmuch as all the anthers crowded together in a particular spike usually open simultaneously, all the scales of the spike in question have their backs covered with the pollen-dust at the same time (fig. 233 [3]). As long as there is no wind the pollen rests on the scales where it has been deposited; but the moment a gust of wind shakes the boughs and twigs of the Pine-tree the pollen is removed from its resting-place, and whole clouds of yellow dust may be seen being blown upward from the spikes (*cf.* fig. 233 [4]).

The corresponding adjustment in the Yew (*Taxus*) differs to a certain extent from the above which is so characteristic of Pines and Firs. The connective of the anther-lobes in *Taxus* does not terminate in an upturned scale, but in a little circular shield with an crenate margin. The anther-lobes are attached to the under surface or back of this shield (see fig. 234 [1]). Moreover, the anthers are united into roundish heads, and the peltate connectives lock closely together like the separate parts of a mosaic, so that the pollen-sacs are not visible superficially. When the pollen has reached maturity and has assumed the form of powder, the pollen-sacs concealed underneath the shields burst open, their walls shrivel, and the anthers have then the appearance portrayed in fig. 234 [2]. The shields now resemble cupolas, supported by short columns, and arching over spaces in which is stored a heap of loose powdery pollen. Under the influence of a warm, dry atmosphere the tissues of the shields contract somewhat, and in consequence chinks appear between the shields, and the spherical conglomeration of anthers seems to be rent asunder (see fig. 234 [3]). When the branches of the Yew are caused to sway by a gust of wind a portion of the pollen is at once blown out through these chinks in the form of a little cloud. In the evening when the atmosphere becomes damper, as also on dull and rainy days, the shields lock together again, and such pollen as is left is once more inclosed and protected from wet. On the return of warm, dry weather the cracks reappear, and the remainder of the pollen may be shaken out and blown away.

The mechanism which has here been described in the case of the Yew, that being an easily accessible example, is found to exist in its main feature, though with many varieties of detail, in the Juniper, in Cypress, and Arbor Vitæ (*Juniperus, Cupressus, Thuja*). One species of Juniper, viz.: *Juniperus Virginiana*, in which the little heads of stamens are closed when the atmosphere is damp, and open when it is dry, has been already selected for illustration in figs. 226 [15, 16, 17, 18], p. 125. Curiously enough, the Planes (*Platanus*), which are not related to the Conifers just referred to, exhibit similar characteristics in the matter of pollen liberation. The stamens have a peltate or pulvinate connective spread out over the anthers, and each stamen, considered by itself, resembles a short peg or nail with a large, thick head. Besides bearing little papillæ, which are looked upon as abortive petals, the globular receptacle of the inflorescence supports a large number of these peg-shaped stamens. They stand out in all directions from the sphere, and their peltate connectives have their edges in contact as in the case of the Yew. Similarly, also, cavities are formed beneath the roof, composed of the connectives, and serve as temporary resting-places for the pollen-cells when they are discharged from the dehiscent and shrivelling anthers. The final process of dispersal of the pollen in the form of dust is, however, essentially different from that which occurs in Yew, Cypresses, and Junipers. In Planes individual stamens fall out of the spherical inflorescence, like bits out of a mosaic, and thus gaps are formed which constitute the means of egress from the cavities filled with pollen-dust. The inflorescences are suspended by long stalks, like big beads on a knotted string, and

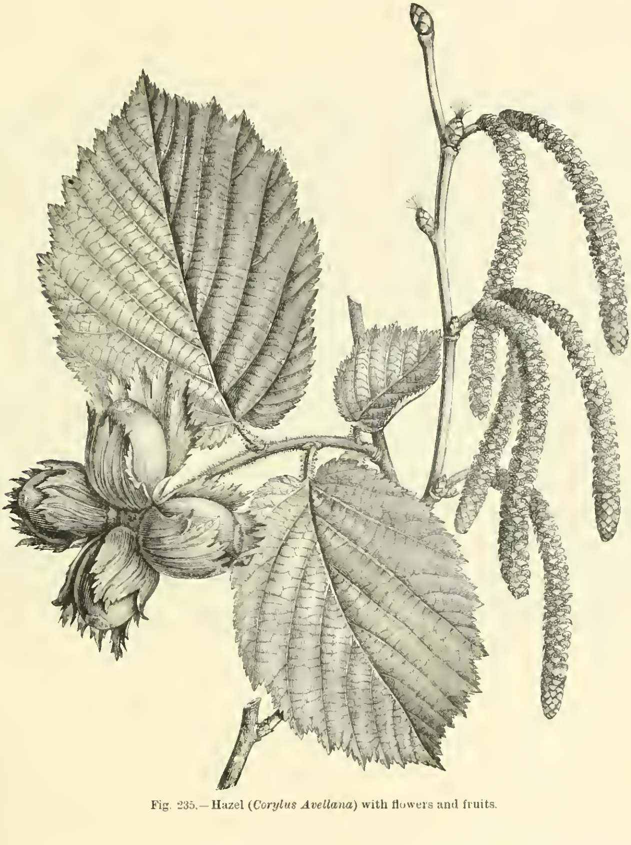


Fig. 235.—Hazel (*Corylus Avellana*) with flowers and fruits.

as soon as a wind sets them in motion the pollen is discharged through the gaps in little clouds.

A temporary deposition of the pollen on the backs of the flowers is common to all the numerous trees and shrubs which have their male flowers aggregated in pendent catkins or spikes resembling tassels or fringes in appearance, as, for instance, the Hazel (*Corylus*, see fig. 235), the Alder (*Alnus*, see fig. 228), the Walnut (*Juglans*, see vol. i. p. 742), Birches, Poplars, and Hornbeams. The floral spikes of all these plants are erect at first, and in the form of short, thick cones and cylinders. A short time before the anthers burst the axis of the spike elongates and becomes pendent, causing all the flowers seated upon it to assume an inverted position with their originally upper faces turned to the ground and their backs upwards. The back of each flower is so contrived as to catch the pollen falling from the anthers of the flowers above it, and retain it until the tassels are set swinging by a gust of wind, and the pollen is in consequence dissipated (*cf.* vol. i. p. 741).

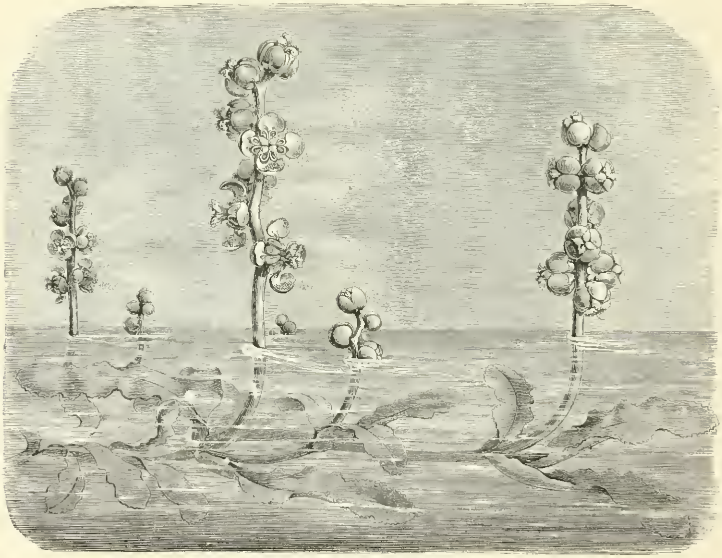


Fig. 236.—Curled Pondweed *Potamogeton crispus*) in the act of pollination.

Sometimes the hollow upper surfaces of sepals, petals, or bracts serve as landing-stages for the pollen when it is discharged. This is the case, for example, in various species of the Pondweed genus (*Potamogeton*), in the Arrow-grass (*Triglochin*), and the Sea-Buckthorn (*Hippophae*). In the Curled Pondweed (*Potamogeton crispus*), a plant which lives submerged in ponds and slow running brooks, and in the height of summer raises its flower-spikes above the surface of the water (see fig. 236), the large, fleshy, reddish-brown stigmas are already ripe to receive the pollen at a time when the anthers close beside them are still closed. The perianth-leaves of the flowers concerned are indeed still folded together, and may be seen underneath the four projecting stigmatic lobes which are arranged in a cross, whilst the anthers are hidden beneath the perianth. The shortly-stalked, concave perianth-leaves do not open back until the stigmas have begun to wither. Almost at the same instant longitudinal slits are formed down the large, white anthers, and they are speedily converted into gaping fissures, out of which flows a copious supply of yellow pollen of mealy consistency. If a fresh, dry wind is blowing at the moment of the dehiscence of the anthers part of the pollen is at once carried off from the spikes of the Pondweed as they project above the water; but if a calm prevails a certain amount of the pollen drops into the cavity of the particular perianth-leaf immediately below the anthers. Here the pollen may remain for hours together if there is no wind. It is only blown away by a strong puff of wind, and is then conveyed directly to other spikes projecting out of the water whose flowers happen to be in a much earlier stage of development, the four radiating stigmatic lobes being in a receptive condition, but the anthers yet indehiscent and the perianth-leaves still closed (see fig. 236).

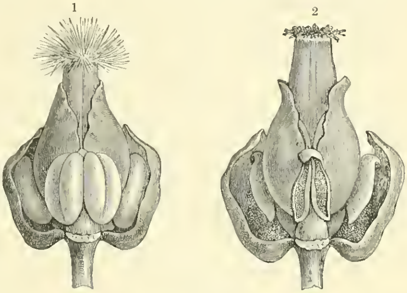


Fig. 237.—Arrow-grass (*Triglochin palustre*).

1 A flower with brush-like stigma already mature; all the anthers still closed. 2 A flower with the stigma withered whilst the three inferior anthers have opened and are depositing their pollen in the concave perianth-leaves at their bases. In both flowers the lower front perianth-leaf has been cut off. × 8.

A still more striking instance of the temporary storage of pollen in concave perianth-leaves is found in the Arrow-grass (*Triglochin*). Here, too, the development of the stigmas precedes that of the anthers by two or three days. During the whole period that the brush-like stigma at the top of the ovary is sound and in a receptive condition the anthers are closed, and they only open when the stigmas have faded and turned brown (*cf.* figs. 237[1] and 237[2]). The stamens, six in number, are in two whorls of three each, situated one above the other (*cf.* vol. i. p. 646), and underneath each stamen there is a deeply-concave perianth-leaf. As soon as the anther opens the pollen rolls into the receptacle thus prepared beneath it, whilst in the meantime the perianth-leaf has moved a little away from the axis and somewhat loosened its connection with it. The pollen rests in its hollow until a puff of wind sets the slender floral spikes swaying to and fro and blows away the pollen. It is a noteworthy circumstance that all six anthers of a flower do not open at once, but that first the lower whorl of stamens comes into play, and that after their pollen has been carried away by the wind as above described both the empty stamens and the perianth-leaves at their bases drop off. Only after this has happened does the upper whorl of perianth-leaves relax; the anthers of the three upper stamens burst open, their pollen glides into the bowl-shaped perianth-leaves below, and exactly the same process is repeated as took place in the case of the superior whorls.

The case of the Sea-Buckthorn (*Hippophae*; *cf.* figs. $220^{2,3,4,5}$, p. 109), is worth mentioning as a third example of the same nature. The flowers of this shrub are conglomerated in little tufts on the sides of woody branches. Each male flower is composed of four stamens and two opposite concave scales; the latter have their edges in contact, so that they form a little bladder within which the four stamens are concealed. The pollen is of an orange-yellow colour and mealy consistency, and is set free from the anthers at a time when the bladder is still closed. It falls into the cavity, and is there completely sheltered from rain and dew by the overarching scales. When a warm, dry wind sweeps over the shrubs the bladders open by two opposite chinks, and the pollen is blown out from its resting-place in small quantities at a time. In damp weather the two scales close up quickly and protect what remains of the pollen from wet; on the return of dry weather they move apart again, leaving a free passage for the wind, which then carries off the rest of the pollen. This simple mechanism ensures the safety of the pollen in the event of rain, whilst enabling it to reach the stigmas of neighbouring shrubs whenever the external conditions are propitious.

A close connection exists between these various contrivances to ensure that pollination shall only take place at the best possible moments, and the maintenance of a free passage in the direction in which the pollen is to be transported by the wind, and further between these adaptations and the shape of the stigmas devised for the reception of the pollen. It is obvious that no barrier must be interposed in the path of the little clouds of pollen-dust on their journey to the stigmas. If the flowers of the Arrow-grass, of Pondweeds, or Grasses were wrapped in large foliage-leaves a great part of the pollen would adhere to these leaves and would be as irretrievably wasted as if it had fallen to the ground or into the water. On this account also all flowers which have their pollen blown out of them by the wind are arranged in spikes and panicles at the upper extremities of the shoots and project freely into the air, but are never clothed with a mass of foliage. Particular attention may be drawn to the fact that a large number of plants wherein the pollen is in the form of dust flower before coming into leaf; that is to say, yield up their pollen to the wind at a time when the green foliage is still folded up in the buds or is just emerging from them. The Sea-Buckthorn, the Alder, the Ash, the Elm, the Hazel, the Birch, and the Aspen all flower and discharge their pollen at a season when the branches are bare of leaves (*cf.* the illustrations on pp. 109, 135, 138, 143, and 147). Were these plants to begin to blossom after the complete development of their extensive foliage the wind-transport of the pollen would be rendered almost impossible. The way to the stigmas would be stopped by innumerable barriers, and the pollen would inevitably be deposited upon these obstacles and stranded.

As regards the stigmas, we find that in plants with dusty pollen they are invariably fashioned so as to catch the dust. In one case they are fleshy and swollen and have the surfaces which are exposed to the wind covered with a velvety coating (see fig. 236), in another they are in the form of tufts of long papillose or capillary filaments, as, for instance, in the Paper Mulberry-tree (*cf.* figs. 229[1] and 229[6], p. 137); sometimes they assume the shape of delicate feathers (*cf.* fig. 231, p. 139), sometimes of camel's-hair pencils and brushes (fig. 237). At the time when pollination takes place they are always fully exposed to the wind and so placed that when the pollen-cells are blown against them they are caught like midges in a spider's web. Yet, in spite of all these contrivances, it would remain very doubtful whether the stigmas would be dusted with pollen through the action of wind were it not for the concurrence of another circumstance. The wind is but an uncertain means of transport, especially in the case of a passive object incapable of exercising any influence on the selection of a route. It is, therefore, important that the pollen should be disseminated broadcast in as thorough a manner as possible, and this is only possible if the number of pollen-cells is excessively large. Supposing that only two thousand pollen-cells were produced in a Nettle-inflorescence and these were surrendered to be the sport of the wind, it would be only by a lucky chance that a single one of these cells would be caught by the stigmas of a plant at a distance of 5 metres; but, inasmuch as the number of the cells constituting the pollen-dust of a Nettle amounts to millions, the probability of successful pollination is increased to a proportionate extent. If the staminiferous flowers of Conifers, Hazels, Birches, Hemp, or Nettles be picked before the dehiscence of their anthers and placed on a suitable substratum until the anthers open, the mass of pollen-dust which is liberated is quite astonishing. It seems scarcely credible that so large a quantity of pollen could have been developed in anthers which are themselves so small, and the apparent anomaly only becomes intelligible when one remembers that the cells were packed closely together in the anthers, but afterwards lie simply in a loose heap. In years peculiarly favourable to the flowering of Conifers vast clouds of pollen are borne on gentle winds through the Pine-forests, and are often swept right beyond them, so that not only the female flowers, needles, and branches of the trees in question are powdered over with the yellow pollen, but also the leaves of adjoining trees and even the grasses and herbs of the meadows around. In the event of a thunder-shower at such a period the pollen may be washed off the plants and run together by the water as it flows over the ground, and then, after the water has run off, streaks and patches of a yellow powder are left behind on the earth, a phenomenon which has given rise on various occasions to the statement that a fall of sulphurous rain has taken place.

DISPERSION OF POLLEN BY ANIMALS.

If this book were ornamented with pictorial initial letters illustrative of the contents of each section, we should have at the head of this chapter a group of flowers with bees and butterflies swarming round them, whilst into the scrolls of the capital would be woven a representation of the quiet life of field and forest as manifested on bright summer days—a subject which plays a prominent part in the poetic descriptions and pictorial art of all unsophisticated nations. Even in these days, pictures of butterflies fluttering about bright-coloured flowers, or of bees engaged in collecting the materials for their honey-combs, still find an appreciative public. Young people especially take pleasure in subjects of the kind, and, since youth never entirely dies out, there will always be people who prefer to see the beautiful lines and tints of flowering meadow and shady wood depicted in miniature than the bold outlines of a landscape. If, however, mere casual observation of the relations between flowers and their insect visitors is sufficient to cause æsthetic pleasure, and has stimulated people of every age and nationality to the production of works of art, it may be imagined how great must be the incentive to scientific study supplied by a deeper insight into these phenomena, and what extreme pleasure is derived from the successful discovery of the reasons for these wonderful relations, and from tracing their connection with other facts of science. It may be confidently asserted that the careful investigation of the processes connected with the visits paid by insects and other animals to flowers has brought the solution of the main problems of modern science considerably nearer, and we have good ground for hoping that the prosecution of these researches will succeed before long in raising the veil which still conceals the truth in the case of a number of unexplained phenomena

Zoologists are quite justified in their assertion that many of the developments of insects' bodies are correlated with the forms of particular flowers. But equally true is the conclusion to which botanists have arrived that many of the properties of flowers are likewise in correlation with the shape and habits of flower-seeking insects. Now, these flower-loving animals which would perish if for a single year the earth were destitute of blossoms, vary to an extreme degree in size and shape, in the nature of their external coatings, in what they require for nutrition, and in respect of their time of flight, and of a large number of other habits dictated by soil and climate. From the tiny midges to humming-birds, from the thrips, which are scarcely 1 mm. long, and live and die with the flowers, to the gigantic butterflies of Ceylon, Brazil, and New Guinea, whose expanded wings measure 16 cm. across, and which flutter cumbrously from flower to flower, a long and graduated series extends which corresponds with a perfectly similar series in the floral world. The diversities of colour in the creatures which visit flowers, the various kinds of mechanism of flight exhibited by beetles, flies, bees, butterflies and birds, the multiplicity of organs by means of which they extract their food from the flowers, their means of attachment to the blossoms, their fur and bristles for brushing off the pollen, have all their corresponding variations in form and colouring amongst flowers, and consequently there is an equally long and apparently parallel series in the realm of plants.

Contemporaneously with the opening of the earliest spring flowers occurs the escape of the first pioneer butterflies from their cocoons; the same sunny day which rouses hive-bees and humble-bees from their winter sleep, sees the Willow-catkins protrude from their brown bud-scales and offer their honey and pollen to the world at large. Many flowers which open early in the morning are only visited by particular butterflies which forsake their nocturnal haunts at the same hour; as soon as the flowers close at sunset the insects in question also seek their quarters, fold their wings, and remain the whole night fast asleep. Other flowers do not open till sunset, when day-flying butterflies are already gone to rest, and they are visited by Hawk-moths, Silk-moths, Owlet-moths, and other Noctuæ which have remained throughout the day concealed in shady nooks and commence their ramblings when dusk sets in. These instances of the mutual relations existing amongst vital phenomena obtrude themselves annually on the notice of the most superficial observer, and have been described time after time.

We need not occupy ourselves any longer at the present day with an account of the facts themselves, but rather with the inquiry into the causes both proximate and remote of all phenomena which are presented to our wondering senses. First of all, the question arises: what is it that induces insects and small birds to visit flowers, and what advantage accrues to a plant from the visits with which its flowers are favoured? The answer is, that the inducement is in some cases care of young, in others the desirability of securing themselves against dangers from storms, and, most commonly of all, it is the craving for food. Flowers, however, do not provide animals with breeding-places, with temporary shelter, or suitable nutriment without claiming a reciprocal service, but have their parts so adjusted that their visitors become laden with pollen, which is then transported to other flowers and deposited on their stigmas where it initiates a series of changes resulting in the setting of the seeds. The next few pages will be devoted to the elucidation and proof of this general answer by aid of individual instances.

As regards the choice of nests for their young it has long been known that the nocturnal Lepidoptera of the genus *Dianthœcia*, and also some species of the genus *Mamestra* lay their eggs in the flowers of Caryophyllaceous plants, *e.g.*, in those of the Nottingham Catchfly, the Bladder-campion, Ragged Robin, and Common Soapwort (*Silene nutans*, *Silene inflata*, *Lychnis Flos-cuculi*, *Saponaria officinalis*). The eggs, which are brought forth through a comparatively long ovipositor, produce tiny caterpillars which move about freely in the undivided cavity of the ovary, and there enjoy not only complete shelter but suitable nutriment, for they live on the ovules and young seeds which are seated upon the central placenta situated in the middle of the ovary. When they grow up they bite a hole in the side wall of the ovary, creep through it and descend to the ground, where they pass into the chrysalis condition. One may see, frequently, on examining the ripe fruit-capsules of the Catchflies, the perforations by which the moth-larvæ have gained their freedom. If the caterpillars of *Dianthœcia* devoured all the seeds in the ovaries, the species of plants frequented by them would derive no benefit, but, on the contrary, an injury from their visits. Owing to the large number of ovules, however, they are very seldom completely destroyed, and even if all the seeds in one of the capsules were to be consumed there would always be other capsules in the same plant which would develop plenty of seeds capable of germination. The majority of the Caryophyllaceous species here in question, the Nottingham Catchfly (*Silene nutans*, see figs. 238 and 239) amongst the rest, flower at night, their blossoms opening at dusk, remaining expanded all night, and closing at sunrise. This is repeated in the case of each flower at least three times. On the first evening the petals which have hitherto been rolled up and folded in the bud, spread themselves out in rays and bend somewhat back (fig. 239); five anthers are rapidly exserted from the middle of the flower, and these soon afterwards dehisce, become covered with adhesive pollen, and remain the whole night in that condition. In the course of the following morning the filiform filaments bearing the anthers belonging to the outer circle of stamens bend back, and the anthers fall off or, less commonly, are left hanging to the ends of the reflexed filaments in the form of empty shrivelled sacs. The next evening the second whorl of stamens included in these flowers comes into play, and just in the same manner as before, five anthers, which dehisce at nightfall, are exserted from the mouth of the flower and expose their pollen. The third day these stamens likewise bend back and usually let their anthers drop, and when dusk sets in the long velvety S-shaped stigmas, which have till then been concealed inside the flower, are pushed out. Certain changes of position affecting the petals proceed simultaneously with these mutations. It has already been mentioned that the petals rolled up in the bud unfold on the first night, and assume a stellate and reflexed attitude. At this time also the flowers emit a delicate perfume like that of hyacinths, which attracts a large number of nocturnal insects, but only lasts from 8 o'clock in the evening till about 3 A.M. At daybreak the petals begin to roll up again, the operation taking place faster when the temperature is moderately high and the sky clear than when the weather is cold and the sky overcast. In the process of involution the petals fall into longitudinal folds and become wrinkled and grooved, so that they hang like five crumpled bags round the mouth of the flower, and

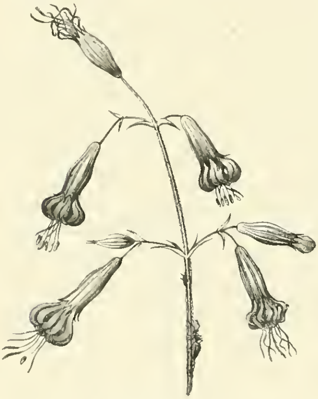


Fig. 238.—The Nottingham Catchfly (*Silene nutans*) in the daytime.

by their appearance might lead one to think that the flower had faded (see fig. 238). But as evening approaches the wrinkles vanish, the petals unfold, spread themselves out into a star, and become slightly reflexed once more. One peculiarity of these flowers is that the inner surface of the petals is white, whilst the outer surface is always of some inconspicuous colour, such as dirty-yellow, greenish, brown, dull red, or ashen-grey. Hence the radiating petals with their white inner surfaces exposed are very striking in the evening darkness, whereas in the daytime the crumpled petals with only their backs visible are anything but conspicuous, and give the impression of being already brown and withered, as may be seen in fig. 238. They are consequently not noticed by insects in the daytime and receive no visits from them.

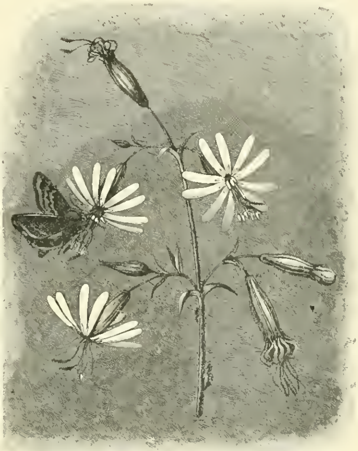


Fig. 239.—The Nottingham Catchfly (*Silene nutans*) by night, a flower being visited by the moth *Dianthœcia albimacula*.

This appears to be exactly what is aimed at. Such insects as visit flowers by day in order to suck their honey would be the reverse of welcome to the Catchfly. The filaments are reflexed, the anthers shrivelled and empty or dropped, and there is no pollen in the flower to be brushed off. A honey-sucking insect could not either take up or deposit pollen in the daytime, and the honey would therefore be sacrificed in vain. Indeed, the flowers would be worse off inasmuch as, being despoiled of their honey, they would possess one less means of attraction in the ensuing night. On the approach of night the pollen-laden anthers and velvety stigmas appear in front of the entrance to the interior of the flower where the honey is concealed, the scent and white colour act as allurements, and the visits of insects are welcome, provided the size of their bodies is such that they rub against the pollen or stigmas and fly quickly from one flower to another. Those which are too small, or are destitute of wings, are still kept at a distance, this being effected by means of contrivances which will be the subject of discussion later on. Of all the welcome species the best adapted in respect of size and shape of body, length of proboscis, and various other structural characteristics are the Owlet Moths (Noctuæ), and of these in particular those of the genus *Dianthœcia*, one of which is represented as visiting the flower of the Nottingham Catchfly in fig. 239. These little moths pay frequent visits to suck the honey whilst the females also lay their eggs in the flowers. It sometimes happens, too, that the females become loaded with pollen from a flower upon which they have rested and taken a meal of honey, and that afterwards they fly with the pollen to other flowers where, instead of sucking any more honey, they lay their eggs, and in so doing dust the stigmas with their freight. To sum up, the flowers of the Nottingham Catchfly and of other species of Caryophyllaceæ above referred to are adapted to the small Noctuæ of the genera *Dianthœcia* and *Mamestra*, and are visited exclusively, or, at any rate, principally, by those insects. The Noctuæ obtain honey from them, and the females find in them homes suitable for their eggs. The return made by the moths to the plants consists in the conveyance of pollen from flower to flower and the consequent conversion of ovules into seeds which would not be effected spontaneously.

The relations just described occur also among several other groups of plants and Lepidoptera. A number of species of the small blue butterflies belonging to the genus *Polyommatus* stand in the same relation to Leguminosæ and Rosaceæ. The beautiful *Polyommatus Hylas* visits the flowers of Lady's-fingers (*Anthyllis Vulneraria*) and in doing so transfers the pollen from one plant to another. The female lays her eggs in the ovaries of the flowers she visits, and from the eggs issue caterpillars which feed on the young seeds. When mature the caterpillars forsake the ovaries and retire underground to pass through the chrysalis stage. The same relation exists between *Polyommatus Bœticus* of Southern Europe and the Bladder-Senna (*Colutea arborescens*), between *Polyommatus Arcas* and the Great Burnet (*Sanguisorba officinalis*) and in many other cases; only, besides the butterflies named, others alight with a freight of pollen on the flowers of these plants, but do not lay eggs in the ovaries, and only receive honey in return for their conveyance of the pollen, so that these cases are really only partially of the same category.

On the other hand, the life-history of one of the moths living on the capsule-bearing species of the genus *Yucca*, and named *Pronuba yuccasella*, has been made out, and must here be dealt with in some detail, as it affords one of the most wonderful examples of the dispersal of pollen by means of egg-laying insects. The flowers in all species of *Yucca* are arranged in large panicles (vol. i. fig. 154, p. 659), and each is bell-shaped and suspended at the end of a smooth, green stalk. The perianth-leaves, six in number, are yellowish-white and are consequently visible from a considerable distance in the dusk and on moonlight and starry nights. After the flower-buds open, which happens regularly in the evening, the perianth forms a widely-open bell (*cf.* fig. 240 [1]). The dehiscence of the small anthers, which are supported on thick and velvety filaments, takes place simultaneously with the divergence of the petals, and a golden-yellow adhesive pollen is to be seen in the spiral slits of the anthers. Each flower is wide open for one night only; by the next day the free extremities of the six perianth-leaves bend towards one another causing the flower to assume the form of a balloon or bladder with six narrow lateral apertures (fig. 240 [1]). In the twilight and by night, numerous small yellowish-white moths (*Pronuba yuccasella*; see fig. 240 [4]) which have a metallic glitter in the moonlight flutter about the flowers of the *Yucca* plants. The females penetrate into the interior of the wide-open bells and there endeavour to possess themselves of the pollen, not with a view to devouring it, but that they may carry it away. For this purpose they are furnished with a special implement. The first joint of the maxillary palp is lengthened to an extraordinary extent, and its inner surface is beset with stiff bristles and can be rolled up like a trunk (see fig. 240^{5}). It is used to seize the pollen, to conglomerate it into a ball and afterwards to hold it. In a very short time a moth collects by its means a ball of pollen, which is held by the rolled-up palpi close underneath the head and resembles a great crop. Laden with this lump of pollen, which is sometimes three times as large as its head, the

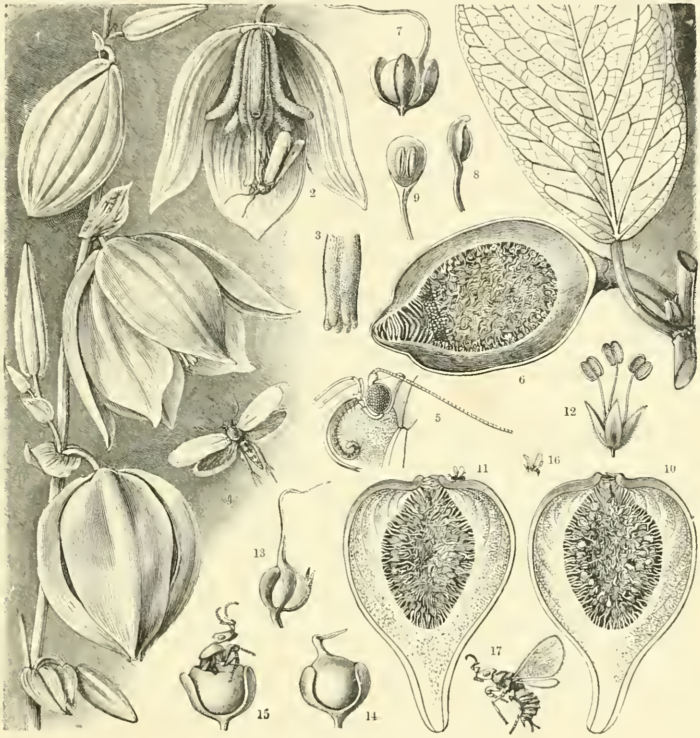


Fig. 240.—Transport of Pollen by Egg-laying Insects.

^{1} Branch from the inflorescence of *Yucca Whipplei*; the middle flower open, that beneath it was open the previous night and is now closed again, the rest of the flowers in bud. ^{2} Single flower of the same plant visited by a moth of the species *Pronuba yuccasella*; the three front perianth-leaves removed. ^{3} Stigma of *Yucca Whipplei*. ^{4} *Pronuba yuccasella* flying to a flower of *Yucca Whipplei*. ^{5} Head of *Pronuba yuccasella* with a ball of pollen held by the coiled maxillary palp. ^{6} Twig with inflorescence of *Ficus pumila*; the urn-shaped inflorescence (or synconium) cut through longitudinally. ^{7} Single female flower from the bottom of the synconium of *Ficus pumila*. ^{8}, ^{9} Stamens of the same plant from the upper part of the synconium. ^{10} Synconium of *Ficus Carica* full of gall-flowers produced by *Blastophaga*, cut through longitudinally; near the mouth of the cavity is a Fig-wasp (*Blastophaga grossorum*) which has escaped from one of the galls. ^{11} Synconium of *Ficus Carica* full of female flowers, cut through longitudinally; near the mouth of the cavity are two Fig-wasps, one of which has already crept into the cavity whilst the second is about to do so. ^{12} Male flower. ^{13} Long-styled female flowers of *Ficus Carica*. ^{14} Gall produced from a short-styled gall-flower. ^{15} *Blastophaga grossorum* escaping from a gall. ^{16} A liberated *Blastophaga*. ^{17} The same magnified. ^{1}, ^{2}, ^{4}, ^{6}, ^{10}, ^{11}, ^{16}, natural size; ^{3} × 2; ^{5}×20; ^{7}, ^{8}, ^{9}, ^{12}, ^{13} × 5; ^{14}, ^{15}, ^{17} × 8.

moth abandons the despoiled flower and seeks another forthwith. Having found one, it circles nimbly round it, making a sudden spring off and on, and ends by settling on two of the thick reflexed filaments, sprawling its legs out upon them. It then seeks to reach a favourable spot on the surface of the pistil with its ovipositor and there deposits its eggs. The ovipositor is composed of four horny bristles, and is adapted to pierce through the tissue of the pistil. After the eggs are laid and the ovipositor is withdrawn, the moth darts to the top of the infundibuliform stigma (fig. 240[3]), unrolls its trunk-like palpi, and stuffs the pollen into the stigmatic funnel, moving its head to and fro repeatedly during the operation (fig. 240[2]). It is alleged that the same moth repeats the processes of alternately laying eggs and stuffing the stigma with pollen several times in the case of the same flower.

Most of the eggs introduced into the pistil are deposited in the vicinity of the ovules. They are of oblong shape, narrow and transparent and increase rapidly in size, soon revealing in each a coiled-up embryo. On the fourth or fifth day the larva is hatched and at once begins to devour the ovules in the cavity of the ovary. Each grub requires from 18 to 20 ovules to nourish it during the period of its development. When it is grown up, it bites a hole in the still succulent wall of the ovary, crawls out through the aperture, lets itself down to the ground by a thread, burrows into the earth and spins an oval cocoon underground in which it remains till the following summer. Fourteen days before the time of flowering of the *Yucca*, it begins to show signs of life, and the moment the flowers of that plant open the silvery moths escape from their pupal envelopes.

An important element in the interpretation of the relations subsisting between the *Yucca* and the *Yucca*-moth is the fact that without the assistance of insects the sticky pollen of the plant in question could not get to the stigma. In the case of *Yucca aloefolia* alone there seems to be sometimes a transfer of pollen to the stigma through the instrumentality of the petals or of the elongating filaments; but in most species of this genus, that is to say, in those wherein the fruit is capsular, this certainly does not take place. With the exception of the moth referred to, insects but seldom fly to them, and those which alight by chance on the flowers do not cause a deposition of pollen on the stigmas. If it were not for the transport of the pollen by *Pronuba yuccasella* the ovaries and ovules of *Yucca* would not ripen into fruits and seeds. As a matter of fact, all the fruits of the capsular species are rendered abortive if moths are kept away from the flowers by means of a gauze covering. Also, in gardens where there are no *Yucca*-moths, the production of fruit is suppressed. *Yucca Whipplei*, which in California, its native land, is visited by a particular moth and develops an abundance of dehiscent capsular fruits, has repeatedly flowered in the Botanic Gardens of Vienna, but the moth does not exist in the gardens, and, in consequence of its absence, not a single fruit has ever ripened there. On the other hand, it is ascertained beyond a doubt that the grub of the moth in question lives exclusively on the young seeds of these species of *Yucca*, so that one is forced to the conclusion that the moth stuffs the pollen into the stigma in order that its grubs may be supplied with the nutriment requisite for the preservation of the species—nutriment which would not be forthcoming unless the ovules were fertilized.

This inference does not, of course, involve the assumption that the operations in question are carried out deliberately by the moth with an intelligent foresight of the results. But there is no objection to our looking upon the habits of these insects as unconsciously purposeful. The stuffing of the pollen into the stigmatic funnels is neither more nor less wonderful than the fact that in remote valleys where the population is very sparse and there are very few vegetable gardens, the cabbage white butterfly often flies miles away to look for cabbages upon which it may lay its eggs so that the grubs may find the food that suits them the moment they are hatched. Equally marvellous, too, is the case of many kinds of caterpillar which spin their cocoons on the bark of trees, and cover the structures wherein they are subsequently to undergo transformation into the chrysalis-state with lichens and fragments of bark, that their temporary resting-place may not be noticed by insectivorous birds; and again the same sort of phenomenon encounters us in the case of the caterpillars which live in the interior of the hard parts of plants, and before transforming themselves into pupæ make a special exit ready for the soft and delicate imago subsequently to be liberated.

It must be observed that the grubs of *Pronuba yuccasella* do not eat up all the developing seeds of the ovary in which the moth lays her eggs. There are about 200 ovules in each ovary. Even if half or two-thirds of them are consumed, there is still a sufficient number of uninjured seeds left to be scattered abroad when they have reached maturity, whereas without the intervention of the moth not a single seed capable of germination would have been produced. Whether or not symbiosis with moths also occurs in the species of *Yucca* bearing berries has not been ascertained for certain; but seeing that the berry-producing species, *Yucca aloefolia*, *Y. Treculeana*, &c., have been found to have holes in all their mature fruits—at least when they are growing in their native countries (Florida, Carolina, Mexico, Louisiana, Texas)—and other traces have been discovered pointing to their having been occupied by caterpillars, the probability is very strong that such is the fact.

Still more remarkable than the relation between the genus *Yucca* and its companion moth is that existing between Fig-trees and certain small wasps of the group of the Chalcididæ. To understand the relation clearly, it is first of all necessary to examine the construction of the inflorescence in the Fig. Looking at a fig that has been cut open lengthwise, as is shown in fig. 240 6, it is observed that it is not a simple flower, but rather a whole collection of flowers inclosed in an urn or pear-shaped receptacle. These pear-shaped shoots are in reality hollow inflorescences bearing numerous flowers on their inner walls. Each fig is termed a synconium. The orifice of the urn is very small, and is further straitened by the presence of small leafy scales. The flowers, which are very simple in structure, almost fill the entire cavity; they are of two kinds, male and female.

Each male flower is composed of one or two—rarely from three to six—stamens, which are supported by scales, and are borne on a short stalk (fig. 240[12]). In many species, as, for instance, in *Ficus pumila*, the stamens are spoon-shaped and have the anthers imbedded in the concavity of the spoon (figs. 240[8] and 240[9]). The female flowers possess a unilocular ovary containing a single ovule. The style is inserted rather to one side of the ovary and terminates in a stigma, which is variously formed. At the base of the ovary are to be seen a few small scales which vary in number, and may be regarded as the perianth (see figs. 240[7] and 240[13]). Many species have two kinds of female flower in the same urn or syconium, viz. some with long styles and developed stigmas, and some with shorter styles and abortive stigmas. The latter are called gall-flowers for a reason that will presently be explained (fig. 240[14]). The relative distribution of male and female flowers is very different in different species. In the inflorescences of the India-rubber Fig (*Ficus elastica*), figured on p. 755, vol. i., the male and female flowers are apparently mixed together promiscuously; in that of *Ficus pumila* (fig. 240[6]) female flowers only are found in the lower part of the cavity, and only male flowers near the mouth. This distribution is the most usual, but yet another difference exists in respect of the number of male flowers. In the synconia of many species the male flowers occur in large numbers near the orifice, whilst in others there are very few—indeed it even happens sometimes that there is an entire absence of male flowers in one inflorescence or another. In many species some individuals only produce inflorescences containing female flowers, and other individuals inflorescences with male flowers near the orifice and with female flowers lower down. But the most remarkable circumstance of all is that in the inflorescences of many species all or most of the female flowers below the male ones are transformed into gall-flowers. This is the case, for instance, in the common Fig-tree (*Ficus Carica*) cultivated in Southern Europe, a species which includes two kinds of individuals, viz. those whose inflorescences contain female flowers only, and those whose inflorescences contain male flowers near the opening and gall-flowers lower down (*cf.* figs. 240[10] and 240[11]). The former individuals are known by the name of *Ficus*, the latter by the name of *Caprificus*.

We have now to consider what may be the meaning of the gall-flowers. As the name indicates, not fruits but galls are produced from these modified female flowers, and this happens in the following manner. There is a small wasp belonging to the Chalcididæ, a family of Hymenoptera (*cf.* fig. 240[16] and 240[17]), already referred to as *Blastophaga grossorum*, which lives upon the Fig cultivated in the south of Europe. This insect passes into the cavity of the inflorescence through the orifice, and there sinks its ovipositor right down the style-canal of a flower, and deposits an egg close to the nucellus of the ovule. The white larva developed from the egg increases rapidly in size and soon fills the entire ovary whilst the ovule perishes. The ovary has now become a gall (fig. 240[14]). When the wasps are mature they forsake the galls. The wingless males are the first to emerge, and they effect their escape through a hole which they bite in the gall. The females remain a little longer in their galls and are there fertilized by the males. Afterwards they come out also (*cf.* fig. 240[15]), but only stay a short time within the cavity of the inflorescence, issuing from it as soon as possible into the open air. They accordingly crawl up to the mouth of the inflorescence, and in doing so they come into contact with the pollen of the male flowers and get dusted all over the body—head, thorax, abdomen, legs, and wings. After squeezing through between the scaly leaves at the mouth of the inflorescence, and having at last reached the outside, they let their wings dry and then run off to other inflorescences on the same or on a neighbouring Fig-tree. I say "run" advisedly, for they but rarely make any use of their wings in this act of locomotion. They now seek exclusively inflorescences which are in an earlier stage of development, that they may lay their eggs in the ovaries. Having found such an one they crawl to the opening and slip between the scales into the interior. Sometimes their wings are injured in the act of entering, indeed, the wings are occasionally broken off altogether, and are left sticking between the scales near the aperture.

Once inside the inflorescence, the wasps immediately devote themselves to laying eggs, and in the process are of necessity brought into contact with the stigmas of female flowers. The wasps are still powdered over with the pollen from their birthplace, and it is now brushed off on to the stigmas, which are thus pollinated from another inflorescence. If the pollen is deposited on normal pistilliferous flowers the latter are able to develop seeds endowed with the power of germination; if it falls on gall-flowers it is, as a rule, ineffectual, because the stigmas are more or less abortive. Moreover, no seeds are formed in these gall-flowers, owing to the eggs of the wasp being laid in their place. In those species of Fig in which gall-flowers are not specially provided, the eggs are laid in a certain proportion of the normally-developed female flowers. It has, however, been observed in the case of the Common Fig (*Ficus Carica*) that eggs of *Blastophaga grossorum* laid in ordinary female flowers do not come to maturity, or, in other words, that a normal female flower is not converted into a gall, even if the wasp in question sinks its ovipositor into it and deposits an egg in the interior. For the style of the normal female flower of *Ficus Carica* (fig. 240[13]) is so long relatively to the ovipositor of *Blastophaga grossorum* that the egg cannot be inserted quite into the ovary, but is left at a spot which is not favourable to its further development and there perishes. The gall-flowers of this species of Fig, with their short styles (fig. 240[14]), are, on the other hand, pre-eminently adapted to the reception of the egg at the spot where the ovule would otherwise develop, whilst at the same time they are not adapted to the production of seeds capable of germination, since no pollen-tubes can develop upon their abortive stigmas. Evidently we have here a case of complementary functions or division of labour in accordance with the following plan. The wasps which deposit their eggs in the figs carry the pollen both to the short-styled gall-flowers and to the long-styled ordinary female flowers, and attempt to lay their eggs in both kinds of flower. The gall-flowers are prepared expressly for the reception of the wasps' eggs, and young wasps actually develop in them; but their stigmas not being adapted to the reception of pollen they do not promote the growth of pollen-tubes, and no fertile seeds are produced. On the other hand, pollen-tubes develop on the stigmas of the long-styled flowers, and the latter produce fertile seeds; but the long-style prevents the proper placing of the wasps' eggs, and consequently galls are never or very seldom produced in connection with these flowers.

It would take too long to discuss all the numerous diversities which have been observed in other species of Fig, even if they were known with sufficient accuracy to admit of a general survey. We will only mention that there are approximately 600 species of *Ficus*, which are distributed over the tropical and sub-tropical regions of both the Old and the New Worlds, and that up to the present time nearly 50 species of small wasps of the genera *Blastophaga*, *Crossogaster*, *Sycophaga*, and *Tetrapus* have been identified as effecting the transference of pollen from one inflorescence to another in the various species of Fig. Thus, for instance, *Blastophaga Brasiliensis* has been identified in the inflorescences of seven different kinds of Fig-tree. For the most part each species of Fig has its own particular wasp; only in extremely rare instances have two different species of wasp been found in the inflorescences of one and the same species of Fig.

In Southern Italy and other parts of Southern Europe where the Fig has been extensively cultivated for ages, the majority of the trees planted are *Ficus*-individuals, *i.e.* such as have female flowers only in their inflorescences, these yielding the best and juiciest figs. Fig-plants of the form known as *Caprificus*, which, besides male flowers, contain only gall-flowers in their inflorescences, are not cultivated, because most of their figs dry up and fall off prematurely. A few specimens of *Caprificus* are reared here and there in order that their inflorescences may be artificially transferred to the branches of the *Ficus*-trees. The process of transference is called *caprification*, and the growers believe that the figs of *Ficus* are improved by the wasps which come out of the *Caprificus*-inflorescences and enter those of the *Ficus*. But this opinion, though very wide-spread amongst cultivators and peasants, is not correct. The figs of *Ficus* do not require the intervention of wasps to become sweet and juicy. As a matter of fact, *Ficus*-inflorescences which have been entirely unvisited by wasps and have developed no fertile seeds in their little fruits, ripen into excellent eating figs, and innumerable quantities of the figs sold come from trees and from districts where no process of caprification is employed. It seems, therefore, that the use of caprification must be traditional and have originated at a time when growers were not only concerned with the production of good fruit but of fertile seeds also with a view to the multiplication of the plants. At the present day Fig-trees are no longer raised from seed but from cuttings, and caprification is consequently superfluous. Nevertheless the country people persevere with the old custom in spite of their ignorance of its real significance.

Flowers and floral envelopes are comparatively seldom called upon to act merely as a shelter for the night, or as a temporary refuge. Most bees and wasps have their own homes which are furnished with safe retreats, and to these they withdraw at dusk and in bad weather, and butterflies, for the most part, are afraid to seek the interior of flower-bells or funnels for any length of residence partly because of their relatively large wings, which are liable to be injured in such confined quarters, and partly because in case of danger a rapid escape from the inside of a flower would be scarcely possible. Only beetles, flies, and Hymenoptera of the genera *Meligethes, Melanostoma, Empis, Andrena, Cilissa,* and *Halictus* need be mentioned; they are essentially nomadic in their habits, not possessing homes of their own or any settled night-quarters, but are satisfied with second-rate shelter, and usually pass the night wherever they have spent the day. If there should happen to be flowers there which offer agreeable food in addition to a warm retreat so much the better. Doubtless it is for these reasons that the honey-bearing blossoms of the Bell-flowers (*Campanula*) and the Foxglove, the interiors of which after sundown have a somewhat higher temperature than the environment (*cf.* vol. i. p. 500), are especially favourite shelters on cold nights. The large capitula of *Crepis grandiflora,* and of several other Composites whose outer ligulate flowers close in the evening, are also sought after by small beetles (*Cryptocephalus violaceus, Meligethes æneus*) and little dark-coloured bees (*Panurgus ursinus*) to serve as nocturnal refuges, because a higher temperature prevails at night inside the closed capitula than outside. At sunrise they abandon their night-quarters, and in doing so probably—in some cases inevitably—brush off some of the pollen which they carry away and take with them on subsequent visits to other flowers.

Sometimes insects remain in comfortable quarters of the kind not only during the night but also during the day, and even for several days. When once the small beetles of the genera *Anthobium, Dasytes,* and *Meligethes* have ensconced themselves in the interior of the flowers of Magnolias or Gentians (*Magnolia obovata, M. Yulan, Gentiana acaulis, G. ciliata, G. Pneumonanthe,* &c.), they do not abandon this comfortable home till the third day. This is also true of the rose-chafers (*Cetonia*), which have a preference for the flowers of *Magnolia grandiflora.* They usually force themselves into the youngest flowers which are only just open and take their fill of the sweet juices exuding on and between the stigmas. Later on they devour also some of the pollen as it is liberated from the anthers and drops upon the petals. When the Magnolia-flowers open under a bright mid-day sun, the Cetonias keep still and warm themselves in the sunshine, and when evening comes, and the upper petals close up, they have no inducement to leave the quarters they have chosen, for the temperature rises in the inclosed space during the night from five to ten degrees Centigrade above the temperature outside, and, besides, the Cetonias are here completely sheltered from the attacks of nocturnal animals. Thus they stay in the flowers until the petals fall off and leave them exposed to the air. The flowers of the Opium Poppy (*Papaver somniferum*) are likewise sought out by flies and beetles as soon as they open, and are not deserted until the petals drop. The sojourn is, however, much shorter than in the case of Magnolia-flowers owing to the fact that the Poppy only closes once for the night and loses its petals the very next day.

In the examples above referred to the insects are not forcibly retained in the flowers, for in fine weather the flowers of Gentians, Magnolias and Poppies are as wide open as they can be. But there are also cases where insects, after slipping into a floral cavity for shelter, are kept there for a time imprisoned. This remarkable phenomenon is exhibited especially by the Aroideæ and Aristolochiaceæ. In many Aroideæ (*Arum, Dracunculus, Helicodiceros,* &c.), of which *Arum conocephaloides* (fig. 241) may be taken as a type, the ensheathing spathe widens out above, whilst below the middle there is a decided constriction, and the lowest part expands into a barrel-shaped receptacle. The temperature inside the cavity is always considerably above that of the environment, and ranges not infrequently from 30° to 36° C.; in the spathes of the Italian Arum (*Arum Italicum*) a temperature of 44° C. has even been recorded (see vol. i. p. 501). All these Aroideæ have an offensive odour of putrefaction, and by this very property attract a number of animals which live on dead bodies and other decaying matter. These creatures settle on the projecting end of the spadix and climb down it into the barrel-shaped cavity, where they find a warm habitation and in addition a supply of food in the thin-walled succulent cells lining the interior. At the part where the spathe is constricted the spadix is encompassed by a ring of stiff bristles, which form a contrivance like a lobster-trap. The points of most of the bristles are curved downwards, so as to allow the insects to climb down into the chamber but prevent their egress. It is not till some days later that the bristles become limp, the constriction in the spathe is loosened and expanded, and the captives are able to leave their temporary prison, and by that time the pollen has been liberated from the anthers and covers that region of the spadix which bears the male flowers; it is thus impossible for insects to climb up the spadix without first becoming loaded with the pollen lying in their way, and they afterwards carry it to other younger flowers. In *Arum conocephaloides* (fig. 241) there are two rings of bristles, one above the other. The upper hairs relax later than the lower ones, and when, after the latter have

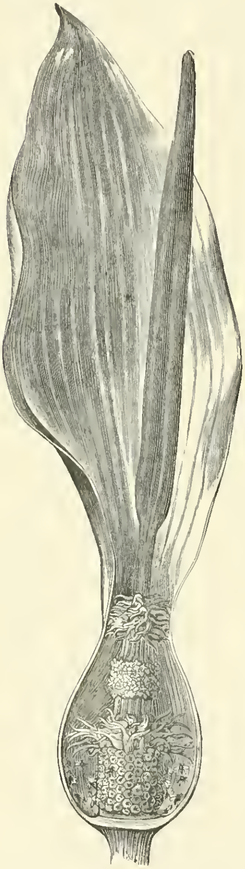


Fig. 241.—*Arum conocephaloides*, with the front wall of the spathe removed. On the lowest part of the spadix are the female flowers, above them the first ring of bristles, next the male flowers, and then a second ring of bristles. At the bottom of the cavity are a number of midges belonging to the genus *Ceratopogon* whose escape is prevented by the stiff deflexed points of the lower ring of bristles.

become flaccid, midges that have been imprisoned at the bottom of the cavity pass into the upper story, they are kept there for a time by the upper bristles, which are still rigid, so that the insects knock against the male flowers and must cover themselves with pollen. Finally, when this object is achieved, the upper bristles also relax and the midges are allowed to escape.

It is astonishing what a large number of insects and what a variety of different kinds find a home in the flowers of Aroideæ. The smaller Aroids, such as *Arum maculatum*, widely distributed in Europe, are sought chiefly by tiny midges of the species *Psychoda phallænoides*, and it is not uncommon to find several hundreds of them in the cavity of a single spathe. In the receptacle formed by the spathe of an *Arum conocephaloides*, planted in the Botanic Gardens of Vienna, three species of small black midges of the genus *Ceratopogon* had congregated, and were present in such large numbers that when one of the spathes was opened artificially a whole swarm flew out. A second spathe of the same plant, which was immersed in alcohol and subsequently opened, was found to contain nearly a thousand midges of the kind. In the Italian Arum (*Arum Italicum*) also as many as sixteen different species of flies, mostly of the genera *Chironomus*, *Limosina*, *Sciara*, and *Psychoda*, have been found in a single spathe. Another Aroid, *Dracunculus crinitus*, is sought principally by large flies belonging to the species named *Somomyia Cæsar* and *Anthomyia scalaris*. In the receptacles formed by the spathes of the *Dracunculus Creticus*, which has flowered in the Botanic Gardens of Vienna, various carrion-beetles (*Aleochara fuscipes*, *Dermestes undulatus*, *Saprinus nitidulus*, &c.) had collected, besides numerous green-gilded flies of the genera *Anthomyia*, *Lucilia*, and *Somomyia*; and in the sheathing-bracts of *Dracunculus vulgaris* which grows in Italy scarcely anything but carrion-beetles of the genera *Dermestes* and *Saprinus* have been observed. A single spathe of the last-named plant was once found to contain more than 250 carrion-beetles belonging to eleven different species.

The flowers of the Birthwort genus (*Aristolochia*) bear a surprising resemblance to the spathes of Aroideæ, their perianths being, like aroid spathes, divided into three regions. First of all, there is the limb, which in the European species has the form of a trumpet, and in the tropical species of America assumes many other curious shapes, as, for instance, that exhibited by *Aristolochia ringens* (fig. 242), where it is drawn out into a boat-shaped under-lip with an upper-lip arching over it. Next comes a tubular median portion, which is furnished with various contrivances to prevent the egress whilst permitting the entrance of creatures seeking shelter. Lastly, there is an enlarged basal portion like a bladder or pouch wherein the stigma and anthers are situated, and which constitutes the goal of the insect-visitors. On a future occasion it will be necessary to enter more fully into the manner in which the insects that creep into the pouch take up and afterwards deposit the pollen, and it will therefore be sufficient to mention here that they are kept prisoners there until the anthers have opened. When dehiscence has taken place, and not before, the tubular middle region undergoes certain changes which make it possible for the captives to escape from their temporary dungeon.

For flowers to serve as refuges and nocturnal haunts for insects they need not necessarily be fashioned into hollow receptacles, pouches, bells, or anything of the kind, as is proved by the following observation. In my garden the flowers of plants of *Phlox paniculata*, indigenous to North America, and of the Canadian Golden-rod (*Solidago Canadensis*), which bloom simultaneously in the autumn, were visited by numberless flies—particularly by the large bee-like *Eristalis arbustorum*—which feasted on as much of the pollen as was accessible to them. By day they stayed as readily on the Phlox-flowers as on the Golden-rod; but as night approached they one and all migrated to the Golden-rod. Not a single fly remained on the Phlox, whereas the great bunches of Golden-rod capitula were covered with hundreds of flies. On the following night, which was still and cold, I examined the flowers by the light of a lantern and found that less dew was deposited on the flowers of the Golden-rod than on those of the Phlox, and this led me to conjecture that the temperature of the former flowers had risen in the night above that of the surrounding atmosphere. And this turned out to be the case. A thermometer inserted in the middle of the inflorescence of the Golden-rod,

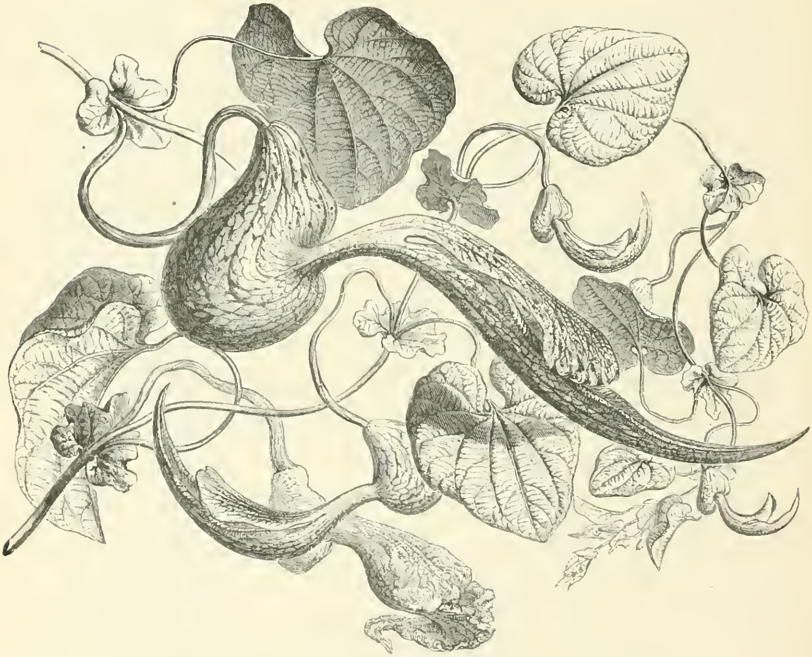


Fig. 242.—*Aristolochia ringens.* (After Baillon.)

which was in full flower, recorded a temperature about 2° higher than the environment, and probably there would have been a still greater difference if the form and disposition of the capitula had not been peculiarly unfavourable to the retention of the warm layer of air in immediate contact with the flowers. The inflorescences of the Phlox exhibited no rise of temperature, but, on the contrary, a fall of 1·5° as compared with the surrounding atmosphere, and they were copiously bedewed. Thus the flies had selected a relatively warm place for their night's rest, although it could not really be called a shelter. As the pollen in the Golden-rod is pushed during the night out of the tube formed by the anthers, the flies found on awaking next morning their meal again ready for them, and it was evidently impossible that they should leave their nocturnal resting-place without first smearing themselves over with pollen.

ALLUREMENTS OF ANIMALS WITH A VIEW TO THE DISPERSION OF POLLEN.

Next to honey pollen is the principal food which animals seek for in flowers. There are some plants from which honey is entirely absent, and which offer only pollen to the food-seeking animals. Such, for example, are the Poppy (*Papaver*), Traveller's Joy (*Clematis Vitalba*), Pheasant's Eye (*Adonis*), and several Anemones (*Anemone alpina, baldensis, sylvestris, Hepatica*, &c.), the numerous Cistuses and Rock-roses (*Cistus* and *Helianthemum*), and Roses (*Rosa*). They all agree in this: that their flowers when open stand erect and have a star-shaped or cup-like form, so that the pollen falling out of the anthers is not lost, but remains for some time on the concave upper surface of the petals. This is especially noticeable in flowers of the Poppy family (*Eschscholtzia, Glaucium, Roemeria, Argemone*; *cf.* fig. 222[1] p. 112, and fig. 243). In comparison with the honey-producing flowers, to be described later on, they always appear to have a simpler construction, which is accounted for by the fact that they have no need of special contrivances for the secretion and storing or protection of honey.

The flowers of these plants are eagerly sought for by little beetles of the genera *Anthobium, Dasytes* and *Meligethes*, and it is no uncommon thing to find in a single Cistus or Rock-rose flower, half a dozen *Dasytes* greedily devouring the pollen. Along with the beetles numerous flies also visit these honeyless flowers for the sake of the pollen, more especially certain Ruscidæ, Stratiomyidæ, and Syrphidæ, which seize the pollen-cells with the terminal lobes of their mouth-parts, bruise them thoroughly, and swallow them bit by bit. Besides these, certain Hymenoptera, *e.g.* species of *Prosopis*, and also Thrips (*Thrips*), are eaters of pollen, and if they establish themselves in great numbers can in a short time almost entirely clear away all there is to be found.

It is well known that bees and humble-bees collect pollen in large quantities and carry it to their nests as food for the larvæ. The collecting is carried on by means of specially constructed hairs and bristles, which clothe various parts of the body, particularly the abdomen and the terminal segments of the hind-legs, and which are sometimes found united into a thick fur, sometimes arranged in regular rows or bands, or grouped into brushes. Some of the hairs are soft and flexible, like delicate little feathers, and when these structures are crowded close together, they act just like a dusting-brush. The pollen over which they have swept, and with which they have become covered, remains hanging between the feathers, from which it can easily be removed afterwards. Other hairs, as already mentioned, are short and stiff, and resemble eyelashes or bristles, arranging themselves in regular rows, so as to form small besoms. In bees and humble-bees these brushes occur on the end-segments of both hind-legs, while in species of *Osmia* only a single brush is formed on the lower side of the abdomen. When these insects stroke the pollen-covered anthers, or the petals on which the loose pollen has fallen, with their legs or abdomen, they remove the pollen with the small brushes and the chinks between the bristles are quite filled with it. Moreover, the bees and humble-bees, with the assistance of the brushes on the terminal segments of their hind-legs, are able to comb and sweep off the pollen which was imprisoned in the soft hairs of their own fur, and thus these brushes form excellent collecting apparatus. In addition, these insects have special contrivances on their legs which have been compared to little baskets; they are smooth, sharply-defined hollows, hedged in by stiff rod-like bristles, in which the pollen, pressed into clumps and pellets, is packed up to be carried home. Many of these Hymenoptera moisten the pollen which they wish to collect with honey-juice, especially if it is powdery or dust-like, so as to be able to knead it into the little baskets. For instance, when the bees wish to obtain the pollen of the Plantain (*Plantago*) as it emerges from the clefts of the anthers, they eject on it first of all some honey from their extended sucking-tube, by which means the loose mass becomes coherent and adapted for collection. It also frequently happens that the loose pollen to be collected is already provided with juices from the perforated, turgid tissue of the neighbouring petals. If the pollen is sticky provision of this kind is not needed. The slightest disturbance and the most delicate touch are then sufficient, and the pollen adheres to the body of the insect, even the smooth hairless parts of the thorax, the abdomen, and the legs being covered with it.

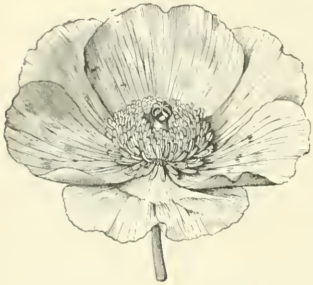


Fig. 243.—Honeyless Flower of *Argemone Mexicana* with abundant pollen.

Since the sole use of insect-visits to flowers is the transference of the pollen from one flower to another, it is evident that some restriction must be placed upon its too extensive demolition. As a great part of the pollen can always be eaten in the flower, or carried off to the nest as food for the larvæ, it is necessary that some should remain adhering to the body of the visitor, so that the stigmas of other flowers may be adequately provided. This necessity is excellently met by the superfluity of pollen. All flowers which contain no honey and offer only pollen as food for the insects, *e.g.* those of Cistuses and Roses, of Poppies and Clematises are characterized by a large number of stamens containing so much pollen that in spite of the extensive depredations of the insects, the necessity of pollinating the stigmas is always provided for. The pollen-eating beetles, after visiting such flowers, are always powdered all over with pollen, and as they cannot immediately rid themselves of that which clings to their thorax, abdomen, wing-cases, and legs, when they leave the flowers, they invariably carry it to other flowers. The bees and humble-bees also, which enter such flowers to collect pollen, come out covered as if with flour, and when subsequently they set to work energetically with their leg-brushes to clear the dust from their fur, there always remains behind enough to give the stigmas of other flowers their portion when they next visit them.

Flowers which conceal honey in their depths are very economical with their pollen, and in them care has been taken that it shall not be squandered or uselessly scattered. Animals which frequent flowers poor in pollen are, moreover, vigorous honey-suckers and do not attempt either to eat the pollen or to collect and carry it into the nest for their brood. Involuntarily, they become streaked and clothed with pollen, a state of affairs not always agreeable to them. At the same time it cannot be very disagreeable, for the animals may be seen immediately after flying out of the pollen-strewing flowers as if frightened, entering flowers of the same species in the next moment where they will experience the same treatment. It would indeed be strange if the same flowers should on the one hand have such contrivances as will allure insects in order that they may transfer the pollen from plant to plant, and on the other hand be so arranged as to shock these laden and attracted guests, and disincline them to further visits. Such a contradiction never does occur in the flower-world, but all the contrivances connected with the transference of pollen display a harmony which fills those who busy themselves with these phenomena with astonishment and admiration.

The dusty, flour-like coatings which are observed on the flowers of some Orchids, particularly of the genera *Eleanthus* and *Polystachya*, are very similar to pollen in outward appearance, but in reality wholly different. They consist of masses of loose, round cells which lie in rows like necklaces of pearls on the upper side of the young petals. As a rule, this covering occurs only on the unpaired leaf of the Orchid-flower known as the lip, which thus resembles a tiny cup filled with flour. The loose cells, which look like flour or dust, contain starch, sugar, oil, and albuminous compounds, and so form an excellent food, serving, just like the pollen-cells, to allure and please the insects.

For the most part these dusty, flour-like coatings are rare. It more frequently happens that rows and masses of cells which project from the surface of certain parts of the flower, appearing to the unaided eye as papillæ, hairs, swellings, and warts, are offered as food to these flower-visiting insects, and must therefore be reckoned so far as allurements. In the flowers of the Portulaca (*Portulaca oleracea*) there is a ring-shaped cushion covering the spherical ovary, from its inner edge spring the stamens, and from its outer margin the petals. Between these two floral whorls the fleshy cushion is seen to be beset with clear, diaphanous papillæ, which, indeed, secrete no juice, but are nevertheless sucked by small insects visiting the flowers, and are sometimes actually eaten. The same is true of the delicate hairs which beset the staminal filaments of the Pimpernel, Mullein, and Spiderwort (*Anagallis, Verbascum, Tradescantia*), and which under the microscope appear to be turgid cells arranged singly or in rows just like the hairs which clothe the bottom of the hollow perianth-leaf in the flower of the Lady's-Slipper Orchid (*Cypripedium*). In several species of the genus *Lysimachia* (*Lysimachia thyrsiflora, ciliata*, &c.), the ovary is covered with small warts whose juicy cells are sucked or devoured by animals; and in the flowers of the Snowflake (*Leucojum vernum*; *cf.* fig. 244), there is a cushion-like mass of cells surrounding the style, whose significance is identical with that of the small warts just mentioned. Numerous Orchids, too, viz. *Odontoglossum, Oncidium*, and *Stanhopea*, bear fleshy swellings, pegs, and combs on their perianths which admit of a similar interpretation.

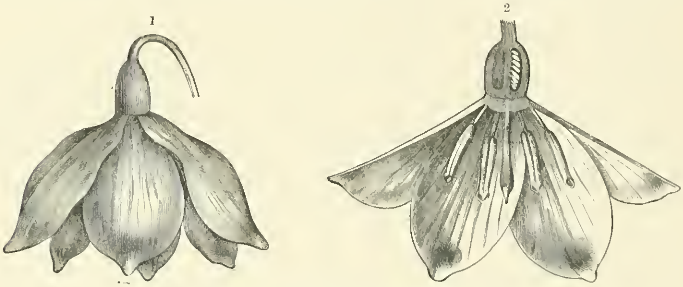


Fig. 244.—Flowers of the Snowflake (*Leucojum vernum*).

[1] Seen from the side. [2] The front part of the flower cut away and the remaining part of the perianth spread out in one plane. Round the style is a cushion of soft tissue which secretes no honey. (Both figures somewhat magnified.)

It also often happens that certain portions of flat petals consist of a cell-tissue which can be easily perforated and sucked by the mouth-apparatus of insects. Such parts are usually distinguished from their surroundings by their greater brilliancy, and one might suppose that this was due to a thin layer of fluid, although this is not really the case. Especially noticeable in this respect are the flowers of *Centunculus minimus*, a tiny Primulaceous plant, whose cup-shaped corolla is carpeted at the bottom with slightly-arched, large, juicy, superficial cells, which glitter like silver in the sun. The petals of the Bloodwort (*Sanguinaria*), of the St. John's Wort (*Hypericum*), of the Laburnum (*Cytisus Laburnum*), of *Spartium*, and of many other plants, behave in the same way. Repeated observations have also shown that the petals of Hyacinths and of many Anemones, and the flowers of the Centaury (*Erythræa*), as well as the hollow, honeyless spurs of our meadow Orchids (*Orchis mascula, militaris, Morio,* &c.), are pierced and sucked by insects, and it should be noted here that not only flies, bees, and humble-bees, but even butterflies are capable of boring into juicy tissue. Butterflies have at the end of their maxillary laminæ which compose their proboscis, certain sharp-pointed appendages with which they first rip up the juicy tissue and then steal the liquid.

A special allurement to those insects which are accustomed to pierce and suck juicy tissues is observed in species of *Eremurus* (*E. altaicus, caucasicus, tauricus*), indigenous in Altai, Caucasus, and Taurus. These plants, which belong to the Liliaceæ, bear a raceme on a long rachis which elongates greatly during flowering. When the flower-buds open the petals are spread out flat, and surround the still closed anthers like a six-rayed star. This only lasts for a short time. As soon as the anthers dehisce and expose their sticky, orange-coloured pollen, the petals roll themselves up, become shrivelled, and form a small dirty red-brown ball, from which spring six thick greenish swellings. These swellings, which are really the juicy veins of the under sides of the petals, resemble green aphides. The fly *Syrphus pirastri,* which is known to seek for Aphides, pierces and sucks these swellings, apparently mistaking them for the insects; at any rate they pierce the rolled-up flowers of *Eremurus* just like Aphides, and, what is most wonderful about the matter, they load themselves by this means with the pollen of the anthers standing in front of the flower, and convey it to the stigmas of other flowers.

We shall have to speak presently of plants whose flowers are only open for a day, a night, sometimes only a few hours. The petals of these plants have this peculiarity, that when they wither they fall quickly, become discoloured, crumpled or rolled up, and pulpy. Then the cell-sap exudes from the tissue and covers the surface with a thin layer of fluid. Pulpy petals of this kind are visited by insects, specially by flies, which lick up and suck the juice, and at the same time cover the stigma with pollen brought from other flowers. This is the case, for example, in *Calandrinia, Tradescantia,* and *Villarsia.* This proceeding is an uncommon one, for the simple reason that the number of plants with such short-lived flowers is very limited.

On the other hand, the secretion of juices on the surfaces of fresh tissues of flowers that remain open several days is a widely-spread phenomenon, so that it is perhaps not too much to say that this secretion occurs in 90 per cent of flowers visited by insects and humming-birds. The secreted juice contains more or less sugar and has a sweet taste. But along with the sugar there are also various other ingredients in solution. According to the variable contents of these ingredients the consistency, the colour, and the smell of the liquid of course vary considerably. Sometimes it is watery and colourless, while at other times it is a thick fluid and brown like treacle. The dark liquid, as it is found in the flowers of *Melianthus,* has an unpleasant and even an offensive odour. But in most cases the smell is similar to that of bees' honey. For the most part this sweet sap is practically the same as honey, and this name is therefore now given to it by most botanists.

Botanists of earlier time called it nectar, and those parts of the flower which prepared and stored it, when they were readily distinguishable, were called nectaries.

The secretion of honey takes place in many cases through stomata, and these are either distributed uniformly over the surface of the tissue, or collected together in particular spots. Usually the stomata are large and of the form known as water-pores. In the Willows (*Salix*) the peg-like or tabular nectary bears only a single large water-pore at its truncated end, which pours out colourless honey. There are also nectaries which are quite devoid of stomata and in which the sweet juice comes to light by diffusion through the outer walls of the superficial cells. Sometimes the inner layer of this cell-wall seems to break down into mucilage, becomes changed into a gummy substance, then into sugar, finally pouring out from clefts in the cuticle which has been raised up like a bladder and burst.

The amount of the honey secreted varies very much. In many plants the drops exuding from the stomata of the petals are so small as to be scarcely visible to the naked eye. In others the honey forms an extremely thin layer, looking as if the tissue had been stroked over with a moist brush. In most cases the small drops flow together into larger drops, which fill the grooves, cylinders, depressions, and cups prepared for their reception. Sometimes these receptacles become filled to overflowing, and then at the least touch the sweet juice flows out of the flowers in drops. This occurs, for example, in *Melianthus major*, growing at the Cape, from whose flowers, with their large cowl-shaped honey-receptacles, an actual rain of honey pours when the inflorescence is shaken. So much fluid honey is secreted by two small horn-like processes in the flower of a tropical Orchid named *Coryanthes*, that it continues to flow for a long time from the points of the horns. The lower end of the so-called lip is hollowed out, and gradually the cavity is quite filled by the trickling honey. The quantity of sweet fluid which so collects amounts to about 30 grammes.

In most instances the most important ingredient of the honey for alluring insects, viz. sugar, is in solution, both on account of its chemical properties and also because the sweet fluid in the hidden grooves and tubes of a flower is thus less exposed to evaporation. Sugar crystals of considerable size formed from the sweet juices of the flower are only found in some Orchids of the genus *Aerides*. It is not necessary to do more than allude to the fact that, as well as in flowers, the sugary solution which pours out from the bracts of certain Composites becomes changed into crumbly crystalline masses, though it may be deserving of short notice. Of this form of sugar as a much-desired food of ants we shall speak in a subsequent chapter.

Usually the honey remains exactly where it has been formed and excreted, but there are some flowers in which this is not so; *i.e.* those where the sweet juice flows from its place of origin and is stored up in special receptacles or honey-bags. This, for example, is the case in the flowers of *Coryanthes*, *Melianthus*, *Viola*, and *Linaria*. It has already been mentioned that in *Coryanthes* there exists an actual collecting-cup, which receives all the honey as it trickles down from the horn-shaped secreting bodies. In *Melianthus* there are two narrow petals from which the honey drops into the cup-shaped sepal. In *Viola* each of the two lower stamens is furnished with a long process which projects from the connective, and these processes excrete honey, which trickles down into the expansion of the lower, middle petal surrounding them. In the Toad-flax (*Linaria*) the honey is excreted by a cushion at the base of the ovary, but flows from it through a narrow cleft between the two longer stamens into the hollow spur of the corolla directed downwards and backwards.

In addition to portions of the flower proper, bracts can secrete honey. In many flowers single members only are changed into nectaries, but in others a whole whorl of members. Tissue-bodies are often seen which are difficult to explain from the standpoint of speculative morphology, because of the incomplete knowledge of their development, and of which it is impossible to say whether they have arisen directly from the receptacle or from a leaf-structure. On this account it is also not easy to classify or enumerate nectaries in a thoroughly satisfactory manner. If, therefore, in the following a certain order is observed, this is only for the sake of distinctness, and not with the idea that the structures placed side by side belong necessarily to one and the same morphological category.

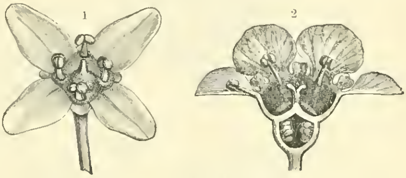


Fig. 245.—Honey-secreting tissue in flowers.

1 Flower of the Spindle-tree (*Euonymus europæus*); ×4 2 Flower of the Red Currant (*Ribes rubrum*) cut through longitudinally; ×5.

In the flowers of most Umbelliferous Plants, of the Cornel, Ivy, Golden Saxifrage, of numerous species of Saxifrage and Spindle-tree (e.g. *Euonymus europæus*, *cf.* fig. 245[1]), a cushion of tissue is developed on the ovary. The stamens and floral-leaves stand round this cushion in a circle but not so as to conceal it, and in the open flower within the corolla the honey may be seen glittering in the sunshine like a thin coat of varnish. The middle of the shallow, basin-shaped flowers of the Sumach (*Rhus*), of the Buckthorn (*Rhamnus*), and of the Red Currant (*Ribes*, *cf.* fig. 245[2]) is covered with a fleshy disc which secretes fluid honey over its whole surface. The Box (*Buxus*) exhibits in the middle of both its staminate and pistillate flowers three little swellings meeting together, each of which deposits a drop of honey. In the Lady's Mantle (*Alchemilla*), *Sibbaldia*, and *Scleranthus* the flower is divided into two stories, into a lower cup-shaped, in which stands the ovary, and an upper, shallower one formed by the floral-leaves. Between the stories is a disc perforated in the middle, or rather a flat ring is interposed which may be compared to the diaphragm in the tube of a microscope. This band also glistens on its upper side in consequence of an extremely thin layer of honey spread over it. The honey-secreting tissue of the Spurge (*Euphorbia*) is very peculiar. The thickly-crowded flowers are surrounded by a cup-shaped envelope whose edge is studded with crescent-shaped, oval, or rounded bodies. These bodies glisten on their upper side with a thin coating of nectar, just like the cushions on the ovaries of Umbelliferous Plants or of the Spindle-tree.

In the flowers of the Sloe, Almond, and Peach trees, Raspberries and Strawberries, some Cinquefoils, and numerous other Rosaceæ, a fleshy tissue is formed around the ovary or its summit, which, spreading from the base of the flower, lines the calyx-tube like a vestment (*cf.* fig. 246^{1}). This tissue secretes honey which, however, is not visible from the exterior, because of the very numerous stamens which surround it and roof it over. In the flowers of Cactuses, also, the lowest cup-shaped or tubular portion is covered inside with a honey-secreting layer of tissue (*cf.* fig. 246^{2} showing *Mammillaria*).

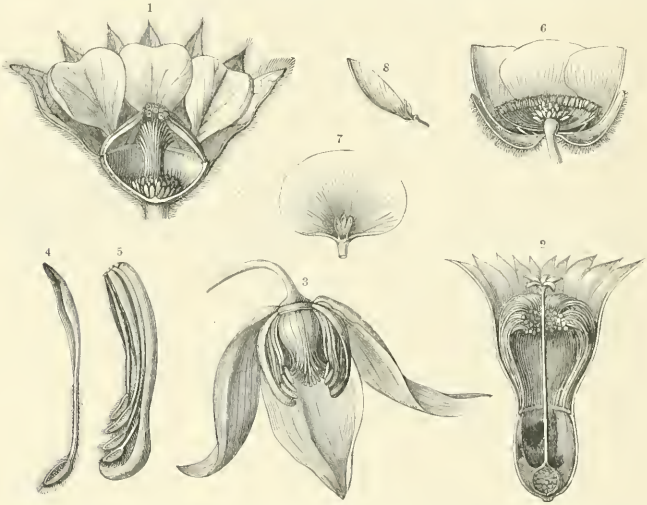


Fig. 246.—Nectaries.

^{1} Flower of Cinquefoil (*Potentilla micrantha*), the front part cut away. ^{2} Flower of *Mamillaria glochidiata*, the front part cut away. ^{3} Flower of *Atragene alpina*, the front part cut away. ^{4} Stamen of the Atragene with trough-like filament (anther downwards). ^{5} Four imbricating trough-like stamens of the same plant held together by a spoon-shaped petal. ^{6} Flower of *Ranunculus glacialis*, the front part cut away. ^{7} A single petal of the same, seen from above. ^{8} The petal cut through longitudinally, seen from the side. ^{3}, ^{6}, ^{7}, ^{8} natural size; the other figs. somewhat enlarged.

In the Thymelaceæ, Scrophulariaceæ, Gesneraceæ, Boraginaceæ, and Labiatæ the honey-tissue forms a wall surrounding the base of the ovary like a ring; while in the closely-allied Rhinanthaceæ, particularly in the genera *Bartsia, Clandestina, Lathræa,* and *Pedicularis,* there is a cushion which is attached to only one side of the base of the ovary, and in *Rhinanthus* and *Melampyrum* at the same point a fleshy, honey-secreting lobe. Moreover, in the Cruciferæ, the tissue surrounding the stalk of the ovary is thickened and swollen, while warts and pegs which secrete honey project from it here and there. In the Stocks (*Matthiola annua* and *incana*), in *Alyssum, Schiverekia,* and *Thlaspi* such warts are seen right and left of the two short stamens, and in *Alliaria* and *Draba* one wart projects from the longer pair of stamens from the outer side facing the corolla. It must remain uncertain whether these structures are to be regarded as part of the stem or as metamorphosed leaves. In many cases—as, for example, in *Haberlea, Pæderota,* and *Polemonium,* where the ring-shaped cushion is divided into five, and in *Scrophularia,* where it is divided into two symmetrically-placed lobes—the appearance is in favour of the latter view. In the flowers of the Bindweeds (Convolvulaceæ) the base of the ovary is surrounded by five thick honey-secreting scales of equal size, which together form a small cup reminding one of an egg in an egg-cup, and in the Crassulaceæ a little knob or a fleshy scale projects from the circular wall of the base of the flower opposite each carpel, sometimes spoon-shaped (*Sedum annuum*), sometimes linear and split at the free end (*Sedum atratum*), and of other varied forms. In these instances the honey-secreting structures are without doubt to be regarded as metamorphosed leaves.

Instances are comparatively rare where the formation of honey is carried on by the carpels—as, for example, the flowers of several Primulaceæ (*Androsace, Aretia*), in which the slightly arched roof of the ovary secretes minute drops of nectar, and in those of many Gentians (*Gentiana acaulis, asclepiadea, Bavarica, Pneumonanthe, prostrata, punctata,* &c.), where the bulb-like, thickened base of the ovary exhibits five cushions which exude abundant honey into the base of the flower-tube. In the flowers of some Liliaceæ and Melanthaceæ (e.g. *Albuca, Ornithogalum, Tofieldia*), the honey is secreted in the lateral grooves of the ovary, and in the flowers of *Anthericum* as well as of *Allium Chamæmoly* a small depression is found on each of the three lines of union of the carpels from which a drop of honey is poured.

Nectaries are found much more frequently on the stamens. They occur there in all sizes and shapes. Sometimes it happens that whole stamens are changed into nectaries, which of course can only be at the expense of the anthers. The stamens of the Whortleberry and Bog-whortleberry (*Vaccinium Myrtillus* and *uliginosum*), like those of Tulips (*Tulipa*), have a small depression which secretes honey on the broad thickened base of the filament opposite the corolla. In the widely-distributed Meadow Saffron (*Colchicum autumnale*) there is an orange-coloured honey-secreting body on the stamens just above the place of union with the violet leaves of the perianth, and the honey there formed fills a channel which traverses the adjoining perianth-leaf. The same thing occurs in other Saffrons and also in the genus *Trillium.* In Geraniaceous plants, especially in *Erodium* and *Geranium,* a wart-shaped, sometimes hollow, nectary arises on the base of each of the five inner stamen-filaments on the side directed towards the sepals. The nectaries at the base of the thread-like filaments of many Caryophyllaceæ exhibit an immense variety of form. Sometimes all the stamens of a flower are a little thickened at their root, and secrete honey from a yellow tissue opposite the ovary (*e.g.* in *Telephium Imperati*), or a pair of honey-secreting warts are found at the base of each filament (*e.g.* in *Alsine mucronata* and *verna*). Sometimes again only the stamens opposite the calyx have swollen bases which secrete honey on the grooved side opposite the ovary (e.g. *Cherleria sedoides*). In the flowers of *Sagina Linnæi* each of the thread-like stamen-filaments opposite the calyx is surrounded at the base by a cup-shaped nectary. Very often the nectaries of adjacent stamens, in the flowers of the above-mentioned plants, fuse together into a ring, the fusion being only just indicated in the Geraniaceæ, but more decidedly in many Caryophyllaceæ (*e.g.* in *Spergula*), and still more amongst Linaceous and Caryophyllaceous plants (*Linum, Gypsophila, Dianthus, Lychnis*). In the flowers of most Papilionaceæ the stamens form the nectar. Nine stamens are fused into a tube in which the ovary is inclosed. This ovary is at the base of the flower narrowed into a stalk, while the tube, on the other hand, is somewhat widened. Thus is formed a cavity into which honey is poured from the adjacent part of the staminal tube. The space is covered over by the tenth stamen, which, however, yields no honey. In *Atragene alpina*, belonging to the Ranunculaceæ, the abundant honey so eagerly sought by humble-bees is formed in the deeply-grooved inner side of the stamens (*cf.* figs. 246 $^{3, 4, 5}$).

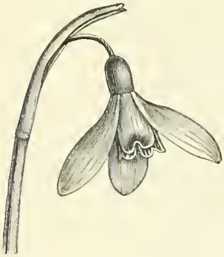


Fig. 247.—Flower of the Snowdrop (*Galanthus nivalis*).

Very often nectar is secreted by the floral-leaves, both in flowers where they form a perianth and also in those where they may be divided into calyx and corolla (*cf.* vol. i. p. 641). In the Snowdrop (*Galanthus nivalis*, see fig. 247), the honey is formed in parallel longitudinal grooves on the inner side of the three outspread perianth-leaves; in Lilies, especially those with hanging flowers and curled perianth-leaves, e.g. *Lilium Chalcedonicum* and *Carniolicum* and the well-known Martagon Lily (*Lilium Martagon*), each perianth-leaf is traversed by a channel studded with bands or ramifying swellings, and filled to overflowing with the abundant nectar secreted in it. Several Orchids, especially species of Twayblade (*Listera*), also exhibit such a channel swollen with sweet sap, but only on one of the perianth-leaves, the lip, which is at the same time the resting-place for the honey-seeking insects while they clear out the channel. In the perianth of the Helleborine (*Epipactis*) the lip is deeply grooved, and resembles a boat filled with honey. In *Epipogium* the perianth-leaf corresponding to the lip is arched like a helmet or cap, and covers the abundant honey there produced. In many other Orchids the lower lip of the perianth is produced backwards, and in the expansion (called the *spur* in descriptive Botany) a quantity of honey is usually hidden. The perianth of *Tricyrtes pilosa* (*cf.* fig. 251 ^{4}) is composed of six leaves, of which the three outer are expanded near their base and secrete abundant nectar. In the flowers of the *Narcissus* (fig. 248), *Gladiolus*, and *Iris*, also in those of *Sisyrinchium* and *Thesium*, the inner side of the tubular perianth is transformed either wholly, or, at any rate, in the lower third into a honey-secreting tissue without the development of any special expansion. The nectaries are unusually well-developed on the perianth of the American *Uvularia grandiflora*, in the numerous species of *Fritillaria*, and especially in the Crown-Imperial, often cultivated in gardens under the name of *Fritillaria imperialis*. Each of the six perianth-leaves in these plants exhibits on the inner side near the thickened base a circular, sharply-defined depression in which sparkles a large drop of honey.

Honey is seldom secreted by the calyx. The best examples are the coloured, expanded and fleshy calyx of the various species of the genus *Cuphea* and of the Nasturtium (*Tropæolum*). The species of the last-named genus have a calyx from whose upper portion a long spur projects. Honey is secreted in the narrowed lower portion of this spur, and indeed so abundantly that it sometimes reaches to the mouth.

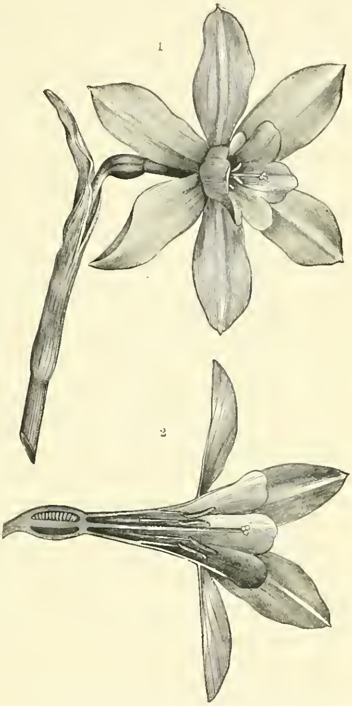


Fig. 248.—Narcissus (*Narcissus Pseudonarcissus*). [1] The complete flower. [2] The flower cut longitudinally.

And now we come finally to the nectaries in the region of the corolla. Those developed at the base of the flower as well as on the carpels, stamens, perianth-leaves, and calyx, though strikingly varied, are poor in comparison with the wealth of forms which are shown in the petals. In this book it is impossible to give an exhaustive description of these structures, and it must suffice to group together generally the most striking forms and those best fitted to illustrate the processes hereafter to be described. In the corollas of the Mulleins, especially in those of *Verbascum Blattaria* and *phœniceum*, the secretion of honey takes place on the large, lower petal in the form of numerous drops scattered over the middle of the leaf. Each drop comes from a stomate, and, therefore, when the flower opens this leaf looks as if it were studded with dew. But this seldom happens. More usually the small drops flow together, and then a large drop appears in some special spot. In the twining Honeysuckles (*Lonicera Caprifolium, etrusca, grata, implexa, Periclymenum*, &c.), in the Bearberries (*Arctostaphylos alpina* and *Uva-ursi*), in *Allionia* and *Crucianella*, in a species of Winter-green (*Pyrola secunda*), as well as in numerous other plants, honey is secreted in the manner just described in the lowest part of the tubular or bell-shaped corolla. In the Alpine Roses (*Rhododen-*

dron ferrugineum and *hirsutum*), as well as in *Monotropa*, the honey-secreting portion of the corolla is thickened and fleshy, and each of the petals, which are fused together, is hollowed into a groove at the base. In the rotate corollas of *Ophelia*, belonging to the Gentian family, each of the petals is provided with a nectar-depression at its base. In the flowers of the non-twining Honeysuckles (*Lonicera alpigena, nigra, Xylosteum*, &c.) the corolla possesses a honey-forming expansion above the base, and in the flowers of the Calceolarias (*Calceolaria amplexicaulis, floribunda, Pavonii*, &c.) the nectary is hidden in the end of the up-turned lower petal as if in a shell. The corolla of the Valerian (*Valeriana globulariæfolia, montana, officinalis*, &c.) manufactures its honey in a small expansion which may be seen on the side of the corolla-tube (*cf.* fig. 249), and in the flowers of the Butterwort (*Pinguicula*) the corolla is narrowed backwards into a pointed spur (*cf.* Plate II. opposite p. 143, vol. i.). In the flowers of the Pansy (*Viola*), only one of the five petals has a honey-collecting spur; in those of the Columbine (*Aquilegia*), on the other hand, each of the petals is drawn out into a spur which develops honey in its club-shaped, thickened end. The small white petals of the Sundew (*Drosera*) terminate at their base in a yellow claw whose tissue secretes a little honey. The same thing occurs in the flowers of the Buttercup (*Ranunculus*), only here the honey-producing tissue is sharply defined and appears as the lining of a circular or oval depression, which, in many cases, is uncovered—as, for example, in *Ranunculus alpestris*—but in others is roofed in by a scale, as in *Ranunculus glacialis* (see figs. 246 [6, 7, 8]). The flowers of *Hypecoum* have two opposite petals, each divided into three lobes, and at the base of these, under the central lobe, a large pit is developed which is filled with the honey abundantly secreted there (see figs. 251 [5] and 251 [6]). The nectaries in the flowers of *Swertia*, belonging to the Gentianaceæ, are very remarkable. Two pits surrounded by a strong circular wall are seen some millimetres above the base of the flower on each petal, and a long fringe like a portcullis hangs down from this wall over the pit. The tissue which forms the lining of the pit develops a quantity of honey, and as the grating does not completely cover the pit the honey may be seen shining through it.

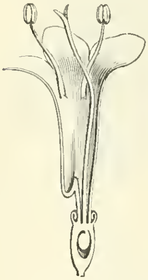


Fig. 249.—Flower of the Wild Valerian (*Valeriana officinalis*), cut through longitudinally.

We must also consider here those remarkable nectaries interpolated between the floral-leaves and stamens of many Droseraceæ, Berberidaceæ, and Ranunculaceæ, to which the name of "honey-leaves" has recently been given. They display the most peculiar forms, and correspond but slightly to the description commonly given of a leaf. For example, in the Grass of Parnassus (*Parnassia*, fig. 267 [5]), belonging to the Droseraceæ, they resemble a hand, on the concave side of which are two honey-secreting depressions, the eleven slender processes which correspond to the fingers terminating in rounded heads. In the flowers of *Epimedium*, belonging to the Berberidaceæ, they are shaped like a slipper. In those of Love-in-a-mist

(*Nigella*), of the Ranunculaceæ, they resemble a covered bowl with a stem, or a hanging lamp (see figs. 250 [4, 5, 6, 7]). In the flowers of the Monkshood (*Aconitum*), they take the shape sometimes of a Phrygian cap, sometimes of a cowl, and occasionally of a French horn, and are carried by a long, erect stalk traversed by a channel. In the flowers of the *Isopyrum* as well as in those of *Cimicifuga*, they resemble shovels or spoons, which carry two puzzling knobbed processes at their free ends. The flowers of the Winter Aconite (*Eranthis*), and of the Christmas Rose (*Helleborus*), exhibit nectaries of a trumpet, cup, or tubular form with obliquely-truncated mouth within the large calyx, and those of the Globe-flower (*Trollius*) conceal numerous spatulate nectaries, which are somewhat bent and thickened in the lower third, where they are provided with a honey-secreting pit (see fig. 221 [3], p. 110). In the flowers of the Pasque-flower (*Pulsatilla vernalis* and *vulgaris*), between the large, flat floral-leaves, and the anther-bearing stamens, small club-shaped structures are interpolated in two or three spiral series. These secrete abundant honey which moistens the base of the neighbouring stamens. All these honey-leaves may be regarded either as modifications of petals or of stamens. Those of *Epimedium*, Love-in-a-mist, Monkshood, and *Isopyrum*, remind one more of the former, those of the Globe-flower and Pasque-flower of the latter. The opinion was stated in vol. i. p. 646, that all perianth-leaves might be metamorphosed stamens, consequently it is idle to inquire whether the honey-leaves are to be regarded as petals or as stamens.

From the point of view of the visits of animals these questions as well as others of speculative morphology are unimportant. But, on the other hand, it is of importance to group together into two divisions those nectaries which we have hitherto but cursorily noticed from a morphological aspect. One of these divisions will comprise the nectaries whose sweet fluid is exposed to the daylight, the other those in which the honey is concealed in hidden nooks at the base of the flower.

The exposed honey is accessible to all flower-visiting animals, but can be appropriated with good results only by some of them. The varnish-like coating of honey, for example, which is spread over the cushion of tissue on the ovary of the Spindle-tree, Ivy and Cornel, Saxifrages and Umbelliferous plants cannot be sucked up by butterflies and humble-bees with long probosces. But it is just this honey which is the centre of attraction for beetles, flies, gnats, and other insects with short probosces. On the flowers of the plants named there are actually swarms of beetles of the genera *Anthrenus*, *Dasytes*, *Meligethes*, *Telephorus* and *Trichius*, as well as innumerable flies and gnats which lick up the thin layer of honey with their tongues or their flatly-extended probosces. And the honey which is displayed in the form of large drops in the depths of the lip of the flowers of the Helleborine (*Epipactis*), and in the corolla of the Figwort (*Scrophularia*) is sought for only by insects with short probosces, particularly by wasps, while it is avoided by humble-bees and butterflies.

With the honey hidden in concealed pits, tubes, and channels, exactly the opposite occurs. This is inaccessible to most of the insects with short probosces but forms the principal food of humming-birds, butterflies, humble-bees, &c. Of course there is again the utmost variety according to the length of the proboscis or bill, and the depth of the hiding-places in which the honey is concealed. The distance of the honey-secreting base from the restricted mouth of the corolla amounts in the flowers of the Heath (*Erica carnea*) to only a few millimetres, while it reaches 16 centimetres in those of the Rubiaceous *Oxyanthus tubiflorus*, which grows in Sierra Leone. In *Angræcum sesquipedale*, a species of Orchid growing in Madagascar and distinguished by the size and splendour of the inflorescence, the perianth possesses a hollow spur 30 centimetres long which is filled with honey at its base.

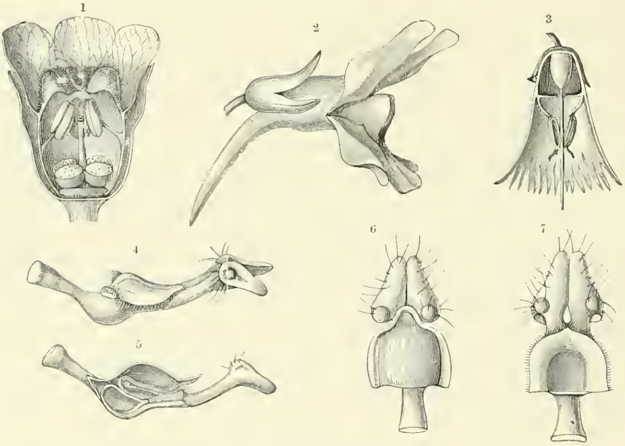


Fig. 250.—Concealment of Honey.

Flower of *Cynoglossum pictum*, the front part of the flower cut away. [2] Flower of *Linaria alpina*. [3] Flower of *Soldanella alpina*, the front part of the flower cut away. [4] A honey-leaf of *Nigella elata*. [5] The same cut through longitudinally. [6] A honey-leaf of *Nigella sativa*, seen from above. [7] The same; the roof covering the nectar-pit cut away. All the figures somewhat enlarged.

There are two kinds of contrivances for hiding the honey in pits, tubes, and channels. In the one the entrance to the hiding-place is narrowed by all kinds of inflations, cushions, bands, and flaps at the mouth of the flower-tube (see fig. 250 [1] of the flower of *Cynoglossum*). In the other the nectary is completely closed over by a roof or door, or by two lips, so that those animals which desire the honey stowed away in the cavity are compelled either to raise the roof, to open the door, or to press down one of the lips. As examples of the latter kind of closing may be instanced the flowers of *Corydalis*, of the Fumitory (*Fumaria*), of the Snapdragon (*Antirrhinum*), and of the Toad-flax (*Linaria*; see fig. 250 [2]), whilst in some Soldanellas (*Soldanella*; see fig. 250 [3]), and in the genus *Aechmea*, belonging to the Bromeliaceæ, the closure is effected by special scales, like folding doors, introduced into the corolla-tube.

Sometimes the stamens are so fashioned and disposed as to form an overarching roof or dome above the honey-secreting base of the flower, *e.g.* in numerous Solanaceæ, Primulaceæ, Boraginaceæ, and Campanulaceæ (*Nicandra*, *Cyclamen*, *Borago*, *Campanula*, *Phyteuma*); very beautifully also in the Willow-herb (*Epilobium angustifolium*), in *Gladiolus*, and in the small-flowered Cinquefoil (*Potentilla micrantha*) pictured in fig. 246^{1}; finally in the Mammillarias, belonging to the Cactaceæ (see fig. 246^{2}).

The hiding of the nectaries by a massing together of the stamens is effected in a very strange manner in some white-flowered Crow-foots, *e.g.* in *Ranunculus glacialis*. In these plants the honey is secreted in small pits on the upper side of the petals close above the yellow, thickened claw (see fig. $246^{6,7,8}$). In front of this pit is a scale which rises from the plane of the petal at an angle of 40°–50°. On and near this scale lie the numerous stamens arranged in several whorls radiating out from the centre of the flower. A small nectar-cavity is thus formed at the base of each petal to which only those insects strong enough to press up the overhanging stamens and the scale can gain entrance. In the flowers of the *Atragene alpina* the stamens are hollowed into a groove in which a quantity of honey is secreted (see fig. 246^{4}). But as in each flower there are many whorls of stamens—those of the outer whorls always covering and being attached to the backs of the inner ones (see fig. 246^{3}), and as all the stamens are held together outside by a whorl of erect, stiff, spoon-shaped leaves (see fig. 246^{5})—all these channels form, as it were, many small, closed, nectar-cavities only to be opened by powerful insects.

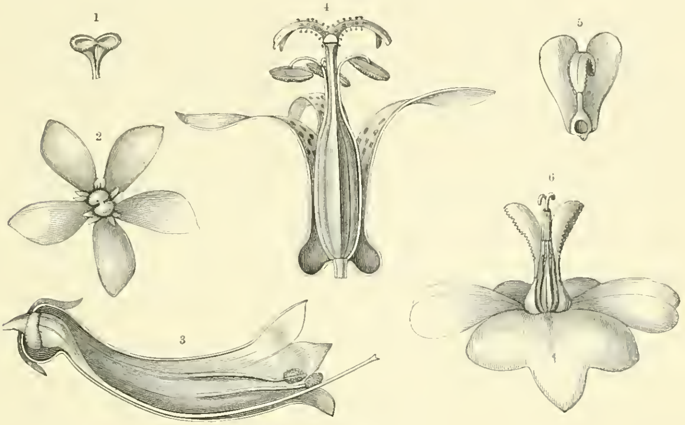


Fig. 251.—Concealment of Honey.

^{1} Stigma of *Gentiana Bavarica* which closes the corolla-tube, removed from the flower. ^{2} Flower of the same plant seen from above. ^{3} Flower of *Phygelius capensis*; the front half cut away. ^{4} Flower of *Tricyrtes pilosa*, the anterior part cut away. ^{5} One of the two inner petals of *Hypecoum grandiflorum* seen from the side adjacent to the ovary. ^{6} Flower of *Hypecoum grandiflorum* showing the two inner petals standing close to the ovary.

The flowers of the *Phygelius capensis* (illustrated in fig. 251^3) show at the base of the tubular corolla a small expansion filled with honey which is converted into a closed cavity by the ovary bending down in front of it and pressing itself closely to the wall of the corolla-tube. In the flowers of *Tricyrtes pilosa* (see fig. 251^4), whose three outer perianth-leaves secrete honey in the expansion at the base of the flower, the three-sided ovary is wedged in like a prop between the perianth-leaves, and three closed nectaries are thus formed out of the expansion. A similar appearance is also observed in the flowers of *Hypecoum procumbens.* Here the honey is secreted in a pit close above the claw of the two inner petals (see fig. 251^5). Just as in *Ranunculus glacialis,* so here, this pit is covered by a peculiar scale which is fitted to receive the pollen at a certain stage of development, as will be afterwards described. This scale is erect and parallel to the ovary, its base being in contact with it (*cf.* fig. 251^6). In this way the pit or nectary is completely closed in.

It may be remarked finally that in many cases the stigma may act as a covering to excavated, honey-containing flowers. This is so, for example, in the Gentians of the group *Cyclostigma*, the flower and stigma of one species of which (*Gentiana Bavarica*) are illustrated in figs. 251^1 and 251^2.

THE COLOURS OF FLOWERS CONSIDERED AS A MEANS OF ATTRACTING ANIMALS.

If we wish that certain distant objects should be plainly seen, it is usual, as is well known, to assist the eye by contrasts of colour. We place signals on the railways with a red band on a white background, put gold letters on black sign-boards, and paint a black circle and a black spot on the white disc towards which we point the gun. The same colour-contrasts occur in plants whose flowers are the aim of flying animals.

Since flowers in most cases open above green foliage-leaves, it is evident why in the floral region those colours are most often met with as allurements which contrast well with green. Of those plants of the Baltic flora whose flowers are displayed against a background of green, 33 per cent are white, 28 per cent yellow, 20 per cent red, 9 per cent blue, 8 per cent violet, and 2 per cent brown. Looked at from a distance white, yellow, and red stand out best from the green of the foliage, blue and violet only a little, and brown scarcely at all.

Usually it is the petals whose colour standing out from the surroundings makes the flowers conspicuous from a distance. That side which is presented towards the flying insects displays the colour most brightly. When the corollas or perianths are pitcher-shaped or bell-shaped, nodding or pendulous, so that the animals on approaching do not see into the inside of the flower, the outside is coloured the more brilliantly. But if, on the other hand, the flower is star-shaped or disc-like, with its face turned to the sky, and to the swarming insects, then the inner side shows the brighter colours. There are even some flowers whose petals are coloured yellow, white, or red on the inside only, while the outer side is green. Those, for example, of *Gagea* are yellow on the inside only whilst the outside is green. When these flowers are closed they do not strike the eye; only when opened in the sunlight does the yellow star show up from the background. The same thing may be said of the flowers of the Star of Bethlehem (*Ornithogalum*), of the Lesser Celandine (*Ranunculus Ficaria*), of the Pimpernel (*Anagallis*), of the Venus's Looking-glass (*Specularia*) and of many other plants.

In some instances where the petals have been transformed into nectaries, or have assumed some other function, which would not easily allow of their developing brightly-coloured surfaces, the duty of alluring the animals is performed by the sepals. These are then not green, but are coloured white, yellow, red, blue, violet, or brown, as, for instance, those of the Christmas Rose and of the white Wood Anemone (*Helleborus niger, Anemone nemorosa*), of the Globe-flower and Winter Aconite (*Trollius, Eranthis*), of the Atragene and of the Monkshood (*Atragene alpina, Aconitum Napellus*), of the Pasque-flower and of the Marsh Cinquefoil (*Pulsatilla pratensis, Comarum palustre*). And of course the features noted above in the case of the petals is repeated in these flowers—the outer side of the calyx is brightly coloured in the hanging bells of the Marsh Cinquefoil, but the inner side in the star-shaped, open flowers of the Pasque-flower.

Nor do the stamens, in comparison with the corolla, calyx, or perianth, frequently serve as attractive organs to animals in virtue of peculiar colouring. In Northern and Central Europe we notice the Willows—destitute of perianth-leaves—rendered conspicuous from afar by their numerous, crowded stamens with red or yellow anthers. In other cases the flowers are conspicuous in virtue of their brightly-coloured stamen-filaments—white, purple, red, or yellow—as in certain Ranunculaceæ, e.g. *Actæa, Cimicifuga,* and *Thalictrum,* still more in the Acacias of Australia, and in the genera *Callistemon* and *Metrosideros* belonging to the Myrtaceæ, in the Japanese *Bocconia,* as well as in several species of *Æsculus* (e.g. *Æ. macrostachya*). The flower-spikes of the North American *Pachysandra,* which trail along the ground, yet stand out from the dark environment because the filaments are dazzling white. In several Asiatic Steppe-plants, viz. in species of *Halimocnemis* (see figs. 252 10 and 252 11), a bladder-like appendage rises above each anther, and is coloured sulphur-yellow, violet, bright or dark red, and thus stands out brilliantly from the gray-green surroundings and might easily be mistaken at first sight for a petal.

It often happens that the bracts which subtend and enfold the flowers rather than the flowers themselves attract attention by the contrast of their colours with the surrounding green. Numerous examples are furnished by the Cornel (e.g. *Cornus florida* and *Suecica*; see fig. 252 12), the Myrtaceæ (*Genetyllis tulipifera*), the Umbelliferæ (*Astrantia, Bupleurum, Smyrnium, Eryngium alpinum*), the Labiateæ (*Nepeta reticulata, Salvia splendens*), Compositæ (*Cirsium spinosissimum, Gnaphalium Leontopodium, Xeranthemum annuum, Carlina acaulis*; see p. 117), the Spurges (*Euphorbia polychroma, splendens, variegata*), the Aroids

(*Richardia æthiopica, Anthurium Scherzerianum*), and the Bromeliaceæ (*Nidularia, Lamprococcus, Pitcairnia*). In some Proteaceæ, e.g. *Protea globosa,* the uppermost foliage-leaves are grouped into a large outer envelope which surrounds the spherical golden-yellow inflorescence, and these crowded leaves are coloured blue in contrast to the lower, scantier foliage, which has a grass-green colour, in order that the inflorescence should stand out the better. Even the stalks of flowers and inflorescences when brilliantly coloured may be seen from a distance and so

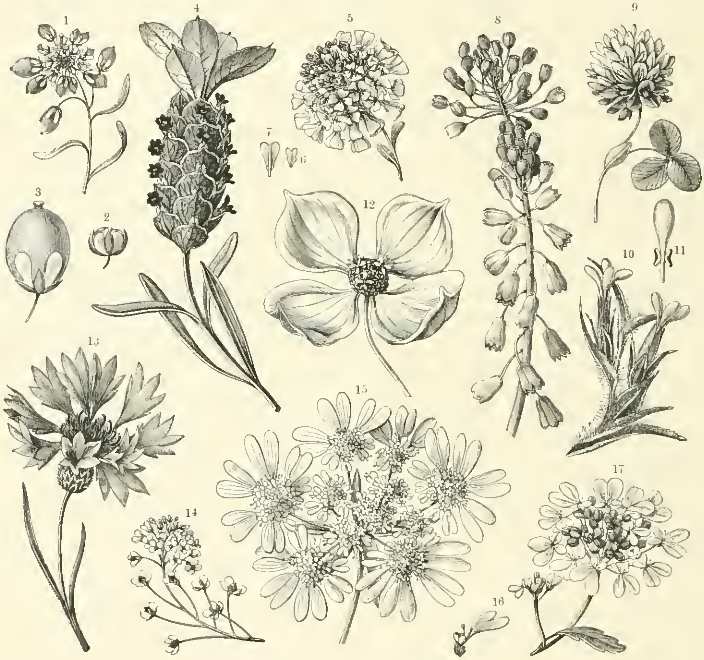
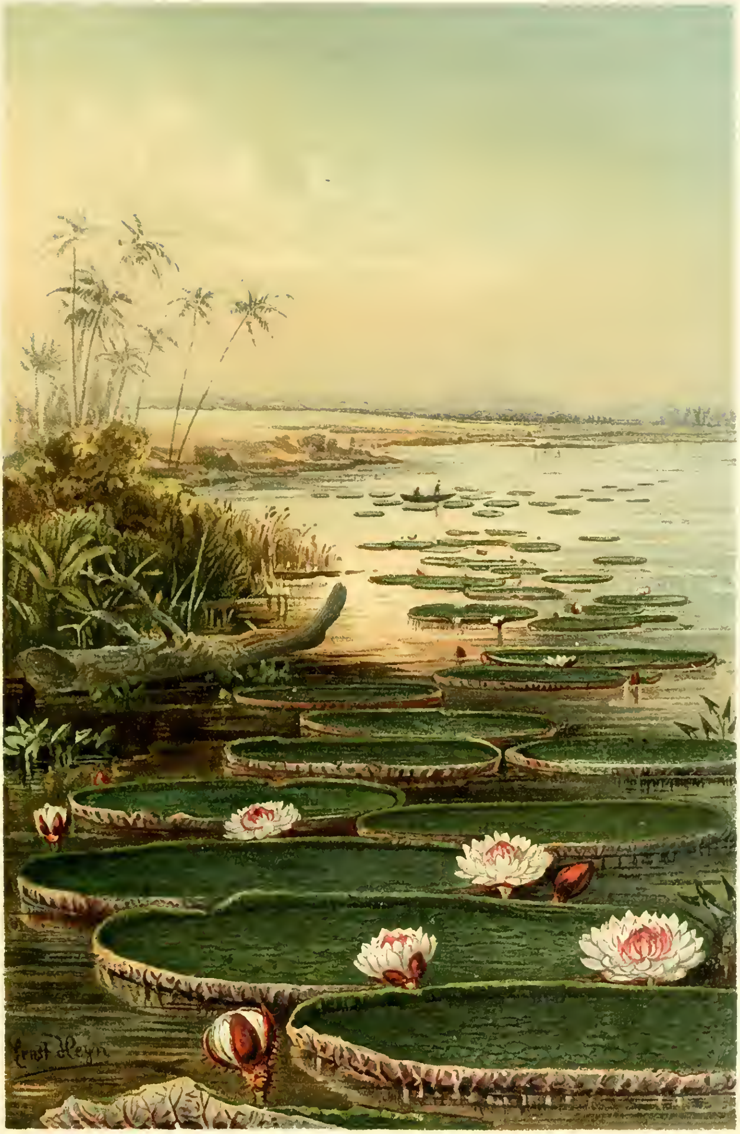


Fig. 252.—Colour-contrasts in Flowers.

[1] Umbellate raceme of *Lobularia nummulariæfolia* with flowers and young fruits. [2] A single young flower of the same plant. [3] A young fruit of the same plant with two of the enlarged white petals attached to it. [4] Flower spike of *Lavandula Stœchas* ending in a crest of empty blue bracts. [5] Umbellate raceme of *Alyssum cuneatum* with young flat open flowers in the centre and old closed flowers at the circumference. [6] Petal of a young flatly-opened flower of the same plant. [7] Petal of an old closed flower of the same plant [8] Raceme of *Muscari comosum*; the upper long-stalked flowers crowded into a head are sterile. [9] Inflorescence of *Trifolium badium*; the upper young flowers are light yellow, the old lower drooping flowers are dark brown. [10] A branch from the inflorescence of *Halimocnemis mollissima*; the erect bladder-like appendages of the anthers protrude from the insignificant perianth and look like petals. [11] A single stamen of *Halimocnemis mollissima*; the connective rises above the anther in the form of a bladder-shaped appendage. [12] Inflorescence of *Cornus florida* surrounded by four large white bracts. [13] Cornflower (*Centaurea Cyanus*); the small flowers of the disc are surrounded by large funnel-shaped sterile flowers. [14] Raceme of *Kernera saxatilis*; the ovaries in the centre of the old flowers are darkly coloured and surrounded by the enlarged petals. [15] Inflorescence of the umbelliferous *Orlaya grandiflora*; the peripheral flowers radiate outwards. [16] A single radiating flower of the same plant. [17] Umbellate raceme of the Candytuft (*Iberis amara*); the outwardly-directed petals of the peripheral flowers are twice as large as those which are turned towards the centre of the inflorescence. [2], [3], [11] are somewhat magnified; the others natural size.



VICTORIA REGIA IN THE RIVER AMAZON

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furnish a means of allurement, as is the case in *Eryngium amethystinum, creticum,* &c., as well as other plants.

When a coloured object is less than a certain size not even the most vivid red, the brightest yellow, or most dazzling white will render it visible at a distance. If the parts of the flower or the envelopes whose function is to attract flying animals from a distance are to be serviceable as signs, they must occupy a considerable space, a necessity provided for in various ways, one of which is the large size of the individual flower. But it would be an error to suppose that this method, from its apparent simplicity, is the most frequent; in point of fact it seldom occurs. Scarcely one in a thousand of the flowers of Phanerogams exceeds 10 centimetres in diameter, and most of these are found only in tropical countries. A species of *Rafflesia,* which has the largest flowers in the world, is illustrated in vol. i. p. 203. The *Rafflesia Schadenbergiana,* which flourishes in the Island of Mindanao in the Philippines at a height of 800 metres above the sea, parasitic on the roots of *Cissus* plants, develops flowers weighing about 11 kilograms a-piece, with a diameter of about 80 centimetres. To be mentioned with these Rafflesias, in respect of extreme diameter, are the flowers of the rare Peruvian orchid, *Paphiopedilium* (*Cypripedium*) *caudatum,* whose ribbon-like lateral petals attain a length of 70 cm. These tailed lateral petals hang down moustache-like right and left of the flower, and though when the flower first expands they are only some 10 cm. long, they continue growing for about ten days, in which time they usually attain their full length. From the second to the seventh day they have been observed to increase in length as much as 5 cm. each day. Very large also are the balloon-like flowers of several tropical American Aristolochias, of which it is stated that children use them in play as caps and pull them down over their heads. Thus the flowers of the Guatemalan *Aristolochia gigas,* var. *Sturtevantii* (cultivated in the Botanic Gardens at Kew) are about 45 cm. wide, 55 cm. long, with a tail exceeding a metre in length; their colour is creamy yellow and deep maroon purple. But of course the amount of substance composing these tailed and inflated flowers is as nothing compared with that which goes to make a huge *Rafflesia*-flower. The flowers of *Magnolia Campbellii* belonging to Sikkim (Himalaya) display almost as great a diameter as those of these tropical creepers. When the erect red flowers of this tree open in the sunshine they show a width of 26 cm., a size never attained by any other tree-flower. One of the Lotus plants, viz. *Nelumbo speciosum,* as well as the Australian *Nymphæa gigantea,* produces flowers with a diameter of 25 cm.; the *Lilium auratum,* recently much planted in European gardens, flowers of 24 cm. Many Cactuses exhibit flowers with a diameter of 20–22 cm., viz., *Echinopsis cristata, Cereus grandiflorus,* the Queen of the Night (*Cereus nycticalus*), shown in Plate VII. (vol. i. p. 641), the South American *Datura Knightii, Nymphæa Devoniensis,* and the celebrated *Victoria regia,* represented in the accompanying Plate XI., "*Victoria regia* in the River Amazon". *Nelumbo luteum, Amaryllis solandriflora,* and the Opium Poppy (*Papaver somniferum*) have flowers of 16–18 cm. diameter, *Amaryllis aulica* and *equestris, Datura ceratocaula* and *Pæonia*

Moutan of 13–15 cm., several Mexican Cactuses (e.g. *Echinocactus oxygonus* and *Tetani*) and the Gourd (*Cucurbita Pepo*) flowers of 10–12 cm. diameter.

Another method by which flowers are rendered conspicuous to the naked eye is the massing together in bunches, spikes, racemes, umbels, and capitula. A single flower of the Elder (*Sambucus nigra*), with a diameter of only 5–6 mm., would be scarcely visible on its dark background at a distance of 10 paces, while a thousand or fifteen hundred of such flowers arranged in a flat nosegay of 16–18 cm. diameter show up quite plainly at the same distance from the dark-green foliage. Even the flowers of the American weed, *Galinsoga parviflora*, recently established in Europe, which are amongst the smallest in the world, having only a length of 1 mm. and diameter of 0·3 mm., become so conspicuous when crowded together in great numbers on a flat disc that they may be easily distinguished by the eye at a distance of 15 paces. The flowers of about 10,000 different Composites, 1300 Umbelliferæ, and innumerable Valerians, Pinks, Stitchworts, Spiræas, Papilionaceæ, and Labiatæ are only visible at a distance because crowded together. If isolated their minuteness would prevent them from being noticed.

Very often it is only a part of the flowers which, when collected into umbels, racemes, and capitula, make the whole conspicuous. In species of *Iberis* belonging to the Cruciferæ (e.g. *Iberis amara, gibraltarica, umbellata*; *cf.* fig. 252 [17]), in most Scabiouses (e.g. *Scabiosa Columbaria, cretica, graminifolia*), and in not a few Umbelliferæ (*Daucus, Heracleum, Orlaya*; *cf.* figs. 252 [15] and 252 [16]), the flowers growing at the circumference of the umbel or capitulum show an enlargement on one side; *i.e.* those petals which are turned away from the centre of the inflorescence are considerably increased and look like short rays proceeding from the periphery. Some Cruciferæ of the genera *Alyssum, Dentaria*, and *Sisymbrium* are also remarkable instances. It cannot be said of these that the flowers standing at the circumference of the umbellate group are really enlarged on one side, yet they have the same appearance as the radiating flowers. This is accounted for by the fact that the petals do not fall off after the deposition of pollen on the stigmas, but remain behind, fold together like the leaves of a book, and, what is still more remarkable, after a little while grow together. When the flowers of *Alyssum montanum, Wulfenianum* and *cuneatum* (*cf.* fig. 252 [5]) reach the highest point of their development, when pollen is formed by their anthers, and honey for insects stored in the flower base, the yellow petals have a length of 3–4 mm.; but when once the anthers have given up their pollen and the flower base is cleared of its honey, when the stigma has dried up and the ovary has already grown into a small fruit, then the petals attain a length of 6–7 mm. (*cf.* figs. 252 [6] and 252 [7]). Thus, while the flowers which have just reached maturity and stand in the centre of the group are small and insignificant, those at the circumference display enlarged petals radiating outwards, thus rendering the whole inflorescence conspicuous. In other words, the older flowers are actually occupied in the allurement of insects for the advantage of the younger ones.

The difference between the peripheral and central flowers of one and the same head does not always consist only in the enlargement of one side, but in many plants in the actual development of different forms of flower. In these the flowers of the centre stand erect and are tubular, while those of the periphery radiate outwards, are larger, coloured much more brilliantly, and are shaped either as short broad plates as in the Milfoil (*Achillea*), or like long narrow tongues as in *Arnica montana*. In the Cornflower (*Centaurea Cyanus*, *cf.* fig. 252[13]) and in allied species the peripheral flowers assume the form of funnels with split edges. One seeks in vain for anthers and stigmas inside these flowers; they have become unfruitful and sterile, and in this way a complete division of function has taken place in the two kinds of flowers of the Cornflower capitulum. Here it is only the flowers of the centre which are provided with stamens and pistils, and which conceal honey at the base of their small tubes; these alone are fertile. On the other hand, they are insignificant in appearance, and at a little distance would not be noticed. Thus the sterile, funnel-shaped flowers, visible from a distance on account of their beautiful azure blue, surround their fruitful neighbours, and perform the task of attracting the insects to them. This remarkable division of labour in flowers of one and the same capitulum seen in Cornflowers may be also noticed in many cymose inflorescences—as, for example, in the Guelder-rose (*Viburnum Opulus*) and in Hortensias (*Hydrangœa Japonica, quercifolia*, &c.; *cf.* fig. 222[8]). Of course only in the wild specimens, for the Guelder-rose grown in gardens, as well as those plants which horticulturists call Hortensias, have inflorescences consisting entirely of sterile flowers from which no fruit can be produced.

While in the last-mentioned plants the sterile flowers which attract insects are found at the circumference of the capitulum or umbel, one meets with a bunch of sterile flowers at the top of the racemose inflorescence in many species of *Muscari*, allied to the Hyacinths (e.g. *Muscari comosum* and *tenuifolium*; *cf.* fig. 252[8]). These are very remarkable on account of their bright colour, and obviously perform the same function on behalf of the less conspicuous fruitful flowers below as do the sterile flowers in the capitulum of the Cornflower.

When the bracts enveloping the flower heads assume the function of alluring insects, and are consequently coloured white, yellow, red or blue, each of these structures singly is usually of such a small size that it could not be seen even at a very little distance; but their aggregate effect is such that the whole inflorescence is conspicuous from afar. The dry scales surrounding the flower-heads are coloured snow-white, golden-yellow, or rose-red in the species of *Helichrysum* known as Immortelles—for example, in the sacred flower which the Greek pilgrims bring with them from Mount Athos (*Helichrysum virgineum*), in the beautiful *Helichrysum frigidum* of the Corsican uplands, in the yellow-headed *Helichrysum arenarium* growing on the sandy heaths of the Rhine valley, and in the numerous species spread over the rocky heights in the Cape. It is evident that the effect of the scaly, coloured envelopes is materially increased when the flower-heads they surround are massed together in numbers forming dense tufts. It thus happens that inflorescences whose individual parts only measure a few millimetres may be plainly seen at a distance of many hundred paces. Fig. 253 is an illustration taken from nature of the Haastias (*Haastia pulvinaris* and *Sinclairii*), composites which grow in New Zealand on mountains of 1200 to 2000 metres in height, and are a good example of the above. The innumerable flower-heads of this plant are crowded together into hemispherical masses which reach a height of half a metre with the diameter of a metre. Both the scaly envelopes and the flowers are coloured white, and since these Haastias grow on rocky heights upon a background of dark earth and stone they stand out conspicuously from their surroundings. The colonists name these plants "vegetable sheep", often mistaking them, so it is said, for fugitives from their flocks, and take long journeys in order to bring them back, only discovering the true state of the case to their great annoyance when close at hand.

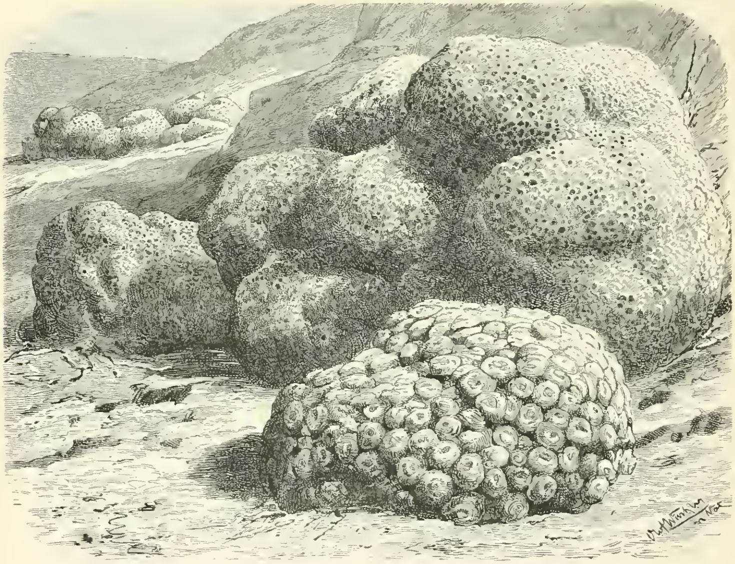


Fig. 253.—Two New Zealand Haastias (*Haastia pulvinaris* and *Sinclairii*, the latter species in front) called "vegetable sheep" by the English colonists in New Zealand.

The bracts of many species of Lavender and Sage (*Lavandula pedunculata*, *Stœchas*, *Salvia viridis*, &c.), growing in the floral region of the Mediterranean, become sources of allurement in a very strange manner. Those which grow beneath the bunches of flowers on the lower half of the spike are insignificant, but at the top, where the flowers are not developed, the bracts are enlarged, brilliantly coloured, and crowded into tufts, resembling the white or red flowers used as trophies by builders to celebrate the completion of a certain stage of their work (*cf.* fig. 252 [4]).

The plants which have hitherto been selected to illustrate the significance of colour in flowers, whether in the blossoms themselves or in their bracts, exhibit only one tone of colour in contrast with the foliage green; that is to say, the entire flower, the whole inflorescence, or the complete group of bracts appears from a little distance as simply white, yellow, red, violet, or blue, and stands out conspicuously from the environment on account of one of these colours. It often happens, however, that the colour-contrast is obtained by the development of several colours in the flowers. In the blossoms of many Willow-herbs (e.g. *Epilobium hirsutum* and *montanum*), the white cross formed by the stigmas appears on a red field; in the Herb Paris (*Paris quadrifolia*) the bright yellow anthers encircle the large, dark-violet ovaries. In the centre of the flowers of the Borage (*Borago officinalis*) a black cone of anthers rises from a blue star, and a yellow cone of anthers on a violet star in the Bitter-sweet (*Solanum Dulcamara*) and in the Potato. In the flowers of the Pheasant's-eye (*Adonis flammea, æstivalis, autumnalis*), the numerous black anthers form a dark centre on a red ground, and an orange centre on a blue ground in the Jacob's Ladder (*Polemonium cæruleum*), whilst in the flowers of the Hepatica (*Anemone Hepatica*) a white centre is seen on a blue ground, and in the flowers of many Mulleins (*Verbascum austriacum, nigrum*) occur stamens with violet hairs which contrast with the light yellow corolla and orange anthers. The dark violet petals of *Saxifraga biflora* surround a centre of golden-yellow, and in the Ice-plant (*Mesembryanthemum crystallinum*), so common at the Cape, the yellow centre formed by the crowded anthers is surrounded by a large number of narrow, radiating, red petals.

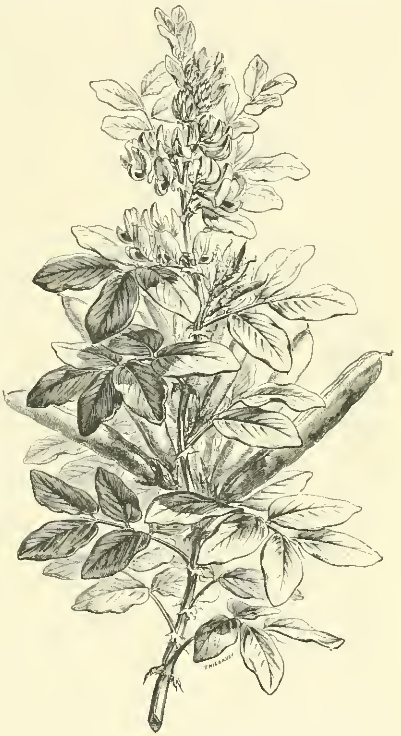


Fig. 254.—Colour-contrast in the flowers of the Bean (*Vicia Faba*). The wings (alæ) of the white papilionaceous corolla are ornamented with large black eye-spots.

In all these instances the stigmas and stamens stand out from the petals, but it may happen that the floral-leaves themselves are thus conspicuous, as, for example, in the flowers of *Victoria regia,* whose outer petals are white, and the inner crimson (see Plate XI. opposite p. 185). In Papilionaceous flowers it is often observed that the upwardly curved petal called the standard is coloured differently from the keel and the wings. The Vetches and Peas (*Vicia picta, Lathyrus odoratus, Baptisia australis*) may be quoted as examples. Those Papilionaceous flowers are most remarkable in which the two lateral wings are dark violet or almost black, and look like two dark eyes below the yellow standard (*e.g.* in *Vicia Barbazetæ, Melanops,* and *Faba*; see fig. 254). In thousands of flowers the petals are marked with spots, speckles, stripes, bands, and borders, the contrasting colours being set next one another. The white perianth-leaves of the Snowflake (*Leucojum vernum*; *cf.* fig. 244) have a green spot near the apex; the scarlet-red standard of the butterfly-corolla of *Clianthus Dampieri* carries a dark-violet eye-spot in the centre; the orange tongue-shaped flowers of *Gorteria ringens* have a black spot at the base, in which are scattered white stripes and dots; the delicate perianths of *Sisyrinchium anceps* are blue or violet above, but yellow or orange below. The white coronas of the Narcissus (*Narcissus poeticus*; *cf.* fig. 255) are surrounded by a cinnabar-red border; and in the blue flowers of the Forget-me-not (*Myosotis*), the mouth of the short tube has an irregular yellow ring round it. Those plants which have been called "*tricolor*" on account of the various tints of their flowers, *e.g.* the three-coloured Bindweed (*Convolvulus tricolor*), the Pansy (*Viola tricolor*), and the three-coloured Vetch (*Vicia tricolor*), may also be quoted as examples.

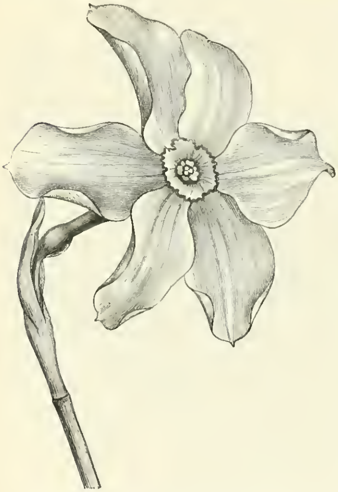


Fig. 255.—Narcissus (*Narcissus poeticus*); the Corona in the centre of the flower is fringed with a cinnabar-red border (black in the figure).

Sometimes the spots, points, and stripes standing up from the ground-colour of the flowers perform the double function of showing the entrance to the honey easiest for the approaching insects, and at the same time most advantageous to the plant itself. Of this we shall speak more particularly later on. But it would be too much to say that all spots are to be regarded as signals or to call them "honey-indicators" or "path-finders". They are found often enough in flowers from which honey is altogether absent, as, for example, in those of *Hibiscus Trionum,* and of the opium and common red Poppies (*Papaver somniferum* and *Rhœas*), where their only use can be to show up the flowers. It should be noted here that flowers with finely-marked petals are ardently sought for, indeed, almost exclusively, by flies. Many Orchids and Labiate flowers, but especially many Saxifrages (*Saxifraga Aizoon, aizoides, bryoides, rotundifolia, stellaris, sarmentosa,* &c.), are very instructive examples. We cannot, indeed, explain what connection there is between the visits of flies and the yellow, red, or violet dots which in some species sometimes change their colour during the period of flowering. But it is certain that the minute red and yellow spots on the petals of these Saxifrages do not make the flowers more visible or conspicuous to the human eye.

A brilliant contrast is caused by the difference in the colours of the corolla and the adjacent outspread bracts and sepals. The flower of *Acanthus,* whose upper sepal is coloured violet, while the petals below it are white, deserves special notice in this connection. Also those of *Clerodendron sanguineum* with white sepals and blood-red petals, as well as the inflorescence of many species of the Cow-wheat (*Melampyrum arvense, grandiflorum, nemorosum*), whose blossoms are yellow and the bracts blue, violet, or red. Lastly, we may mention *Sideritis montana* and *Romana,* whose small, brown petals project like dark points from the yellow bracts.

In the capitula of Composites whose flowers are crowded closely together, the florets of the ray and of the disc usually display different colours. As examples of this common form of colour-contrast may be mentioned the Ox-eye Daisy (*Leucanthemum vulgare*), whose yellow disc-flowers are surrounded by white ray-flowers; *Pyrethrum carneum,* with yellow disc-flowers and red ray-flowers; Rudbeckias and Zinnias (*Rudbeckia laciniata, fulgens, Zinnia hybrida,* &c.), whose dark-brown disc-flowers are surrounded by yellow ray-flowers, and almost all the numerous series of Asters with yellow disc-flowers and blue ray-florets.

Contrast of colour is also frequently produced by the corollas changing their colour at various stages of development. In the bud they are red, after opening they become violet, and then when they wither they become blue or malachite green. When such flowers are crowded together a very effective colour-contrast may result. Especially remarkable in this respect are the Bitter Vetches (*Orobus vernus* and *Venetus*), and several Boragineous plants belonging to widely different genera (e.g. *Pulmonaria officinalis, Mertensia Sibirica, Symphytum Tauricum*), and also some Willows (e.g. *Salix purpurea, repens, Myrsinites*), in which latter the crowded anthers appear at first purple, red, then yellow, and finally black. The tubular flowers of the flat disc-shaped head of Telekia (*Telekia speciosa*) are yellow at first, but later become brown, and since the flowers open successively from the circumference towards the centre of the head, when the blossom is at its height the yellow centre is surrounded by a dark-brown ring. In many species of Clover (*Trifolium*), the faded corollas do not fall off at the end of the flowering period, but wither and dry up, and envelope the small fruit like a mantle. The stalks of the flowers grouped into umbellate heads then bend downwards and arrange themselves into a wreath surrounding the upper, younger flowers which stand erect and are, of course, of a different colour. Thus in the Bastard Clover (*Trifolium hybridum*), the young, erect, densely-crowded, white flowers are surrounded below by a garland of older, rose-red flowers; and in *Trifolium spadiceum*, the light-yellow centre formed by the young flowers is surrounded by a zone of chestnut-brown older flowers whereby a very remarkable colour-contrast is brought about (*cf.* fig. 252 [9]).

The contrasts met with in the umbel-like racemes of the small-flowered Cruciferæ are also extremely varied. These are partly produced by changes of colour during the opening and fading of the flowers, partly by the increase which the petals undergo very noticeably after pollination. In a group of these Cruciferæ of which the Whitlow-Grass, the round-fruited Penny Cress, and the Egyptian Lobularia (*Draba verna, Thlaspi rotundatum, Lobularia nummulariæfolia* (*cf.* figs. 252 [1, 2, 3]) may serve as types, the originally very tiny white leaves of the corolla increase to twice their size, and adhere to the broad side of the ovary, which has meanwhile become much enlarged, and brown or violet in colour. The ovaries, to which the snow-white petals adhere, grow into young fruits, and then form a wreath, just as in the species of Clover described above, around the younger white flowers, as well as the central green buds. The consequence is that the whole inflorescence is rendered conspicuous, although the leaves of the corolla when it opens are small and insignificant.

In a second group of the Cruciferæ, of which *Thlaspi alliaceum* and *Thlaspi arvense* may be chosen as examples, the ovaries as they mature into fruits are only slightly discoloured, but the green of the sepals changes in the older flowers into yellow. Thus in each corymb white, yellow, and green appear side by side in a varied play of colour. A third group, of which *Alyssum calycinum, Draba aizoides* and *Arabis cœrulea*, may serve as types, is rendered conspicuous by the bleaching of the sepals and petals after flowering. The petals of *Draba aizoides* and *Alyssum calycinum*, which, while blossoming, were golden yellow, become whitish and adhere to the young green fruits. The petals of *Arabis cœrulea* are blue at the commencement of flowering, but fade later on and lie flat on the young fruits, which have meanwhile assumed a violet tint. In these three groups of Crucifers the broad side of the maturing ovary serves as a foil to the pale floral-leaves, which increase in size after fading, and thus a piebald effect is given to the whole inflorescence. In a fourth group, of which the Wild Cress (*Æthionema*) is an example, the young fruits are completely enveloped by the enlarging floral-leaves, and are therefore without significance as regards colour. The contrast is here obtained in the following peculiar manner: The young flowers are supported side by side on short, erect pedicels at the top of a common stem, and their small, expanded petals are all turned with their upper side towards the observer. After fading, the pedicels lengthen, bend sideways, and project horizontally from the common stalk of the whole inflorescence. The petals still grow in length and breadth, and place themselves together like the leaves of a book, so that the side which formerly was the lower one is now turned to the spectator. But, since the upper and under sides of the petals are differently coloured, the young flowers crowded in the centre of the corymb exhibit a different colour from the old ones of the circumference. This phenomenon is most beautifully shown in species of this genus which grow in the Taurus (*Æthionema grandiflorum* and *diastrophis*) where the white centre of the corymb is surrounded by an ornamental red wreath of older, folded flowers. The species of the genus Bitter Cress (*Cardamine*), which, together with many other Cruciferæ, form a fifth group, agree with the species of Wild Cress just described in regard to the enlargement and folding together of the petals, but in them the contrast is not brought about by the juxtaposition of the colours on the upper and under sides of the petals, but by a change of colour in the sepals. The sepals, originally green, become coloured yellow in the older, horizontally-placed flowers, but the colour of the petals remains unaltered, white or violet. Finally, in the flowers of a sixth group, of which *Kernera saxatilis* (fig. 252[14]) may serve as an example, the petals of the older flowers do not fold together and do not adhere to the ovary, but retain the position which they had at the beginning of flowering, *i.e.* they always present the upper side to the beholder. But as the flowers get older the ovary swells enormously and becomes coloured a dark purple brown; it pushes itself between the petals, and these (which have increased considerably) now form a white inclosure to the purple fruit. Thus the old flowers at the circumference of the corymb obtain a spotted, conspicuous appearance.

We have now to speak of the colour contrast which comes into play between different kinds of plants growing in the same district, the flowers of which unfold simultaneously. In a meadow studded with thousands of the blue flowers of the *Campanula*, the orange-coloured stars of *Arnica montana* rising up between them show up much more plainly than if these Bell-flowers were not present. The same may be said of the Bell-flowers whose blue colour is materially heightened by the presence of the orange-coloured stars of the Arnica. It might almost be said that the growth of plants side by side with contrasting colours so frequently observed is arranged in the way here indicated, and the change of colour in the flowers of one and the same species in different regions can also be explained by the fact that contrast of colour is so advantageous to the plants in question. Let us suppose that on a meadow where in summer a plant with red flowers—perhaps a Pink—grows in great quantity, a blue Bell-flower has established itself. Some members of it may bear white flowers, as often happens in this plant. Without doubt these white Bell-flowers show up better than the blue from the red Pinks, and therefore have more chance of being visited by insects and of forming fruit and seeds. In course of time the white Bell-flowers will constitute the overwhelming majority, and the meadow will be studded for the most part with white Bell-flower blossoms growing between the Pinks with their red flowers. If the same Bell-flower had established itself in a field in which orange-yellow flowers grew in great numbers, the blue and not the white-flowered plants would have been visited by insects, since they would be the more conspicuous; thus they would multiply and ultimately prevail.

In the neighbourhood of the Brenner *Campanula Trachelium* bears white flowers, but blue flowers in the valleys of the Eastern Limestone Alps. The long-spurred Violet (*Viola calcarata*) displays a blue corolla on the meadows of the Western Central Alps, and a yellow corolla in the Eastern Alps of Krain. *Astragalus vesicarius* has yellow blossoms in the Tyrolese Vintschgau, violet on the Limestone Mountains of Hungary. *Melittis Melissophyllum*, in the Southern Tyrol, has white flowers only; whilst in Lower Austria and Hungary it has purplish-white flowers. The Alpine Poppy (*Papaver alpinum*) occurs on the débris-slopes of the Lower Austrian and Styrian Limestone Alps with white flowers, in those of the South-Eastern Limestone Alps, in Krain, with deep yellow flowers. *Anacamptis pyramidalis*, on the north side of the Alps, is only seen with deep carmine-red flowers; in the Dalmatian Islands and in Italy it exhibits pale flesh-coloured blossoms. *Anemone alpina*, on the Central Tyrolese Alps, bears chiefly sulphur-yellow flowers; in the Eastern Limestone Alps its flowers are always white. The crested Cow-wheat (*Melampyrum cristatum*) displays pale-yellow bracts on its flower-spikes in the Southern Tyrol, but red ones in Lower Austria and Hungary; indeed a long series of plants might still be mentioned which behave in the same way, *i.e.* in which sometimes this sometimes that colour is the more advantageous to the flower, and becomes the prevailing tint in different regions according to the presence of, and in combination with, other plants.

In the descriptions of floral colour, so far given, green has always been regarded as the one which formed the background or substratum from which the other colours and colour-combinations must stand out if they are to be plainly seen by flying animals. As a matter of fact, the ground-tone of the plant-covering during the period of vegetation is mostly green; but in districts where the trees and bushes strip off their foliage in the autumn, and where throughout the winter and spring a mantle of withered leaves covers the ground, the prevailing tint is brown. Similarly, where in the autumn the grasses and various meadow-weeds also wither and fade, the ground-tone of the plant-covered earth in the following spring is not green but pale-yellow or brown. Against such a background obviously the colour-contrasts become somewhat different. Blue colours show up better from a brownish-yellow than from a green background, and it may depend upon this fact that the flowers of so many plants which emerge in spring from the dry withered leaves are coloured blue. The flowers of *Hepatica triloba*, growing in the depths of light woods, are shown up excellently by their blue colour from the yellow-brown Hazel and Hornbeam leafage, but would scarcely be noticed on a green meadow. On ploughed land the flowers of *Omphalodes verna* can be seen 100 yards off over the pale yellow, faded grasses and foliage of the edge of the wood; while at the same distance against a green background they would stand out much less clearly. The same thing is true of many Boragineæ, which grow in similar places (*Pulmonaria angustifolia, officinalis, Stiriaca, Lithospermum purpureo-cæruleum*), of the Lesser Periwinkle (*Vinca minor*), of the Squill (*Scilla bifolia*), and of many others.

Colour-contrasts which differ from those of the green background of land covered with fresh foliage-leaves are also found in shady woodland spots where dark-brown humus has accumulated. Above the dark mould of the forest-floor a pale colour, such as that of the Bird's Nest (*Neottia*), of *Monotropa*, and of the Toothwort (*Lathræa*), and other saprophytic and parasitic plants, is plainly visible from a distance. These plants would hardly be noticed in a green meadow.

Zoologists are of opinion that animals, especially those which visit flowers to carry off honey and pollen, possess a highly-developed colour sense, and that the visits which are paid by bees, humble-bees, butterflies, flies, and beetles are materially influenced by the colour of the flowers. Different animals prefer different colours, and there are actually certain insects to which some colours are "pleasing", others "unpleasing". The favourite colour of the honey-bee, for example, is a deep violet-blue; pure blue and violet are also pleasing to it, yellow is less sought after but not avoided. Towards green the bees are indifferent, but red is disliked and shunned and is the "unpleasing" colour as far as bees are concerned. With regard to blue and violet it is quite true that these colours in flowers act as excellent allurements for humble-bees and bees, especially for honey-bees, and this is the more remarkable since, as already mentioned, blue flowers are not by any means the most numerous. We can only accept the views of zoologists as to red up to a certain point, however. Flowers with purple-red or carmine-red colour, as well as all the shades from these to violet, are eagerly visited by bees, and therefore only scarlet-red, cinnabar-red, and the shades leading from them to orange are to be regarded as unpleasing to them.

In a garden bed close in front of the house where I live in summer a patch of *Pelargonium zonale*, called by gardeners Scarlet Geranium, is planted. Near at hand, on the other side of the path, there grows the narrow-leaved Willow-herb (*Epilobium angustifolium*). The scarlet-red flowers of the Geranium and the violet flowers of the Willow-herb open simultaneously. Bees and butterflies swarm and flutter hither and thither over them, but, strangely enough, the butterflies halt on both these plants and do not show especial preference for either. The honey-bees fly past the scarlet flowers with indifference, and turn only to the violet flowers of the Willow-herb. In the Vienna Botanic Gardens the bluish-violet flowers of *Monarda fistulosa* and the scarlet *Monarda didyma* stand side by side with the blue flowers of the Hyssop (*Hyssopus officinalis*). All three blossom together about the middle of July. The honey-bees fly about there in large numbers, but they only visit the Hyssop and violet-flowered *Monarda*, the scarlet flowers of *Monarda didyma* being avoided by them. I purposely here say "avoided" and not "disliked", because it is uncertain whether the absence of bee-visits to scarlet flowers is caused really by an actual dislike of the scarlet colour, or whether it is not rather colour-blindness which is known to be the reason why many human beings do not see red. If we say that the honey-bees do not see the scarlet colour it would be clear why they would pay no visits to the flowers of the Scarlet Geranium and the scarlet *Monarda*. They would not notice them, because the nerve-bundles which correspond to the scarlet colour are wanting in their eyes. This does not contradict the fact that other animals see this colour well, and that for them a scarlet colour may be an effective means of allurement even from a great distance. Butterflies, as already mentioned, hover over the flowers of the Scarlet Geranium; *Monarda didyma* is industriously visited by a large humble-bee, and various animals are seen to fly to other scarlet-red flowers, especially in tropical regions. Such flowers in particular affect the humming-bird. Indeed it seems that this tiny bird in its search after honey prefers scarlet flowers. Perhaps it depends upon this that plants with scarlet flowers are distributed chiefly in those regions where humming-birds have their home. Certainly it is noteworthy that the scarlet colour is only rarely met with in Asia and Europe, particularly in the Alpine, Baltic, Black Sea, and Mediterranean Floras; whilst an exceptionally large number of such flowers occur in America, particularly in Carolina, Texas, Mexico, the West Indies, Brazil, Peru, and Chili. In the primeval forests of Central America every traveller is struck by the great number of Lianes and Epiphytes of the families Acanthaceæ, Bignoniaceæ, Bromeliaceæ, Cyrtandreæ, and Gesneraceæ, which bear scarlet flowers, and of which we may mention as examples—*Bignonia venusta*, *Lamprococcus miniatus*, *Pitcairnia flammea*, *Nemanthus Guilleminianus*, *Mitraria coccinea*, and *Beloperone involucrata*. Lobelias, Fuchsias, and Begonias with fiery red cups (*Lobelia cardinalis*, *fulgens*, *graminea*, *splendens*, *Texensis*, *Fuchsia coccinea*, *cylindria*, *fulgens*, *radicans*, *spectabilis*, *Begonia fuchsioides*, &c.), the scarlet species of Sage which are surrounded by humming-birds (*Salvia coccinea*, *cardinalis*), the various species of *Alonsoa* and *Russelia* belonging to the Scrophulariaceæ, the remarkable Erythrinas (*Erythrina crista-galli*, *herbacea*, *speciosa*), and the Cæsalpinieæ of the genera *Amherstia* and *Brownea* (*Amherstia nobilis*, *Brownea coccinea* and *grandiceps*), whose flowers are so constructed that their honey can hardly be obtained except by the hovering humming-bird—all these find a home in the American regions above-mentioned. Further observations in tropical regions are required to ascertain whether there are not other flower-visiting animals besides humming-birds and butterflies, especially flies and beetles, which can distinguish scarlet flowers and fly to them; for certain plants, as, for example, the Brazilian Aroids with their large scarlet spathes, *e.g.* *Anthurium Scherzerianum* (the Flamingo Plant), *A. Andreanum* and *Lawrenceanum*, have no honey, and are consequently disregarded by humming-birds and butterflies.

That scarlet flowers are not visited by the hawk-moths, owlet-moths, and other crepuscular and night-flying animals is obvious, since when twilight falls, scarlet, as well as purple-red, violet, and blue flowers become invisible. At this time only those flowers can be seen which are coloured white or yellow on the side turned towards the flying animals, as, for example, the Evening Primrose (*Œnothera*), the Honeysuckle (*Lonicera Caprifolium*), some Nyctagineæ (*e.g.* *Mirabilis longiflora*), many Solanaceæ (e.g. *Nicotiana affinis*, *Datura Stramonium*), numerous Caryophyllaceæ of the genus *Silene* (e.g. *Silene nutans*, *longiflora*, *Saxifraga*), various species of *Yucca* and *Calonyction*, and, most of all, the large-flowered Mexican Cactuses of the genus *Echinocactus* and *Cereus*, of which the species known as

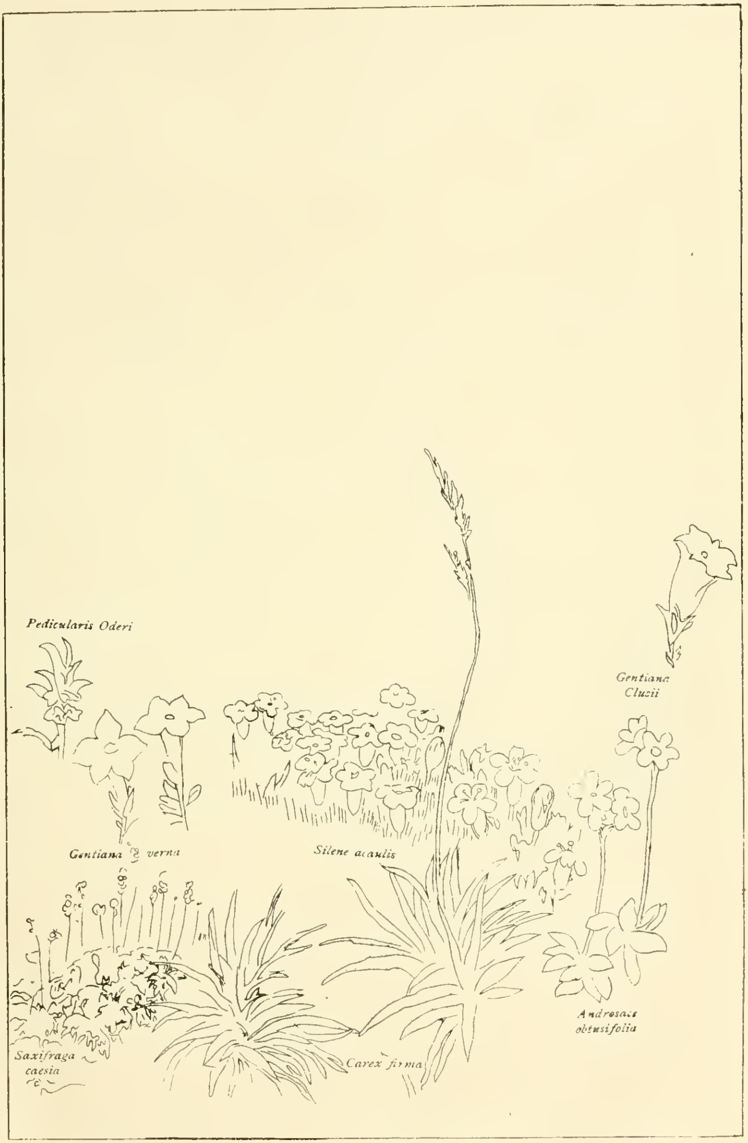
"Queen of the Night" (*Cereus nycticalus*) is shown in Plate VII. opposite p. 641, vol. i. When dark-coloured flowers are visited at night by insects, for example, those of *Hesperis tristis*, *Pelargonium triste* and *atrum*, it is not in consequence of the colour but of the scent of the flowers, as will be described later on. Without doubt, white is the colour which is not only best seen in the dark, but can be plainly distinguished in bright daylight, and it is, as far as we know, not avoided by a single flower-visiting animal. Even those animals which have a badly-developed sense of colour, and can perhaps only distinguish between light and dark, are able to appreciate white, as it is the lightest of all colours. Yellow flowers are eagerly visited by animals which collect and eat pollen, perhaps because the pollen is usually coloured yellow. Greenish-yellow and brownish-yellow flowers, as, for example, those of the Parsley and the Parsnip, of the Aralia and the Ivy, of the Maple and the Buckthorn, of the Rue and the Sumach (*Petroselinum, Pastinaca, Aralia, Hedera, Acer, Rhamnus, Ruta, Rhus*), are especially preferred by flies which swarm over dungheaps and other refuse (e.g. *Lucilia cornicina, Onesia sepulcralis, Sarcophaga carnaria, Scatophaga stercoraria*). This phenomenon has been explained by the similarity of the colours named with those of the dungheap and offal generally. Dark brown must exercise a specially attractive power over wasps. They fly with great haste to brown flowers, especially those whose tint resembles that of decaying pears and other fruit, whilst they will pass by colours which are far more noticeable to other eyes. Flowers of a pale, fawn-red, and dirty violet colour in conjunction with brown, so arranged as to resemble decaying flesh and dead bodies, and such flowers as possess by way of additional attraction a smell of putrefaction, are always visited by carrion-flies and dung-beetles in abundance. It might be thought that the smell alone would suffice to attract these insects; but it must be otherwise, or it is difficult to see why the various Aristolochias, Stapelias, Rafflesias, and Balanophoreæ, which smell like carrion, should bear its colours as well as its scent. It is not easy to decide how much depends upon the colouring, and how much on the scent, and it would be premature to give a definite judgment now. It should be noted generally that the opinions just stated should not be accepted as being entirely free from doubt. Researches on these points are very difficult, and there are so many sources of error that the results may have to undergo many corrections sooner or later. But, on the other hand, all that has been said must not be regarded as quite worthless. This one thing is quite certain—that some animals will show a preference for one colour in a flower, while others will prefer another, and that the absence or presence, the significance or prominence of single floral colours is to be placed on a parallel with the same phenomena in the Animal Kingdom.

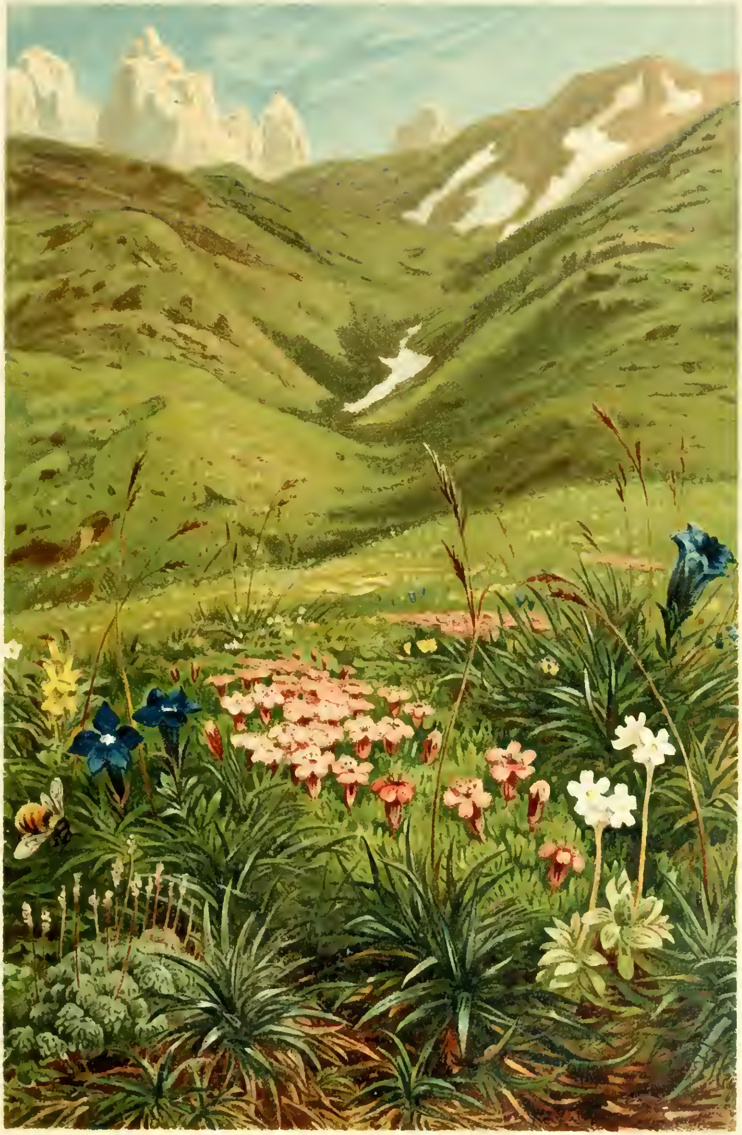
It is extremely probable also that in many floral regions the predominance of certain floral colours at various seasons of the year is connected with the distribution of animals in time, since the insects which fly about in spring and summer, and in summer and autumn differ from one another. It has been shown graphically by curves for the region of the Baltic flora that in April and May a white colour predominates, and that from the highest point in May the curve of white gradually sinks to its lowest point in late autumn. Yellow reaches a first maximum in May, falls somewhat during the summer, and reaches a second maximum in October. The curve of red takes a low position in early spring, rises uniformly through the summer, and reaches its highest point in September. The curves of violet and blue show no large variations through the whole period of vegetation, but two maximal points are to be seen in them, just as in the yellow, one in spring, and the other in autumn.

This particular seasonal change of the prevailing flower-colour, of course, only holds good for the Baltic flora. Even in the adjoining Mediterranean flora the colour-curves are somewhat different, and the deviations are greater still in the flora of corresponding latitudes in North America. Nothing can be said of the predominance of certain colours during the vegetation period in the Alpine flora, for on the heights above the tree-line there is actually no spring and no autumn, only a short summer following a long winter. All the flowers have therefore to blossom in this short time, and all the flower-visiting animals must do their flying about during the short period which is free from snow, if they do not wish to starve. Hardly is the snow melted when there appear almost simultaneously the violet bells of the Soldanellas and the golden flowers of the Cinquefoil (*Soldanella* and *Potentilla*), the white Crowfoot and Androsace, the red Silenes and Primulas (*Ranunculus alpestris, Androsace obtusifolia, Silene acaulis, Primula minima*), the blue Gentians and the yellow Auriculas (*Gentiana acaulis, verna, Primula Auricula*), the heaven-blue Forget-me-not and the yellow Violet (*Myosotis alpestris, Viola biflora*) as well as the Saxifrages in every conceivable colour. On looking at the varied flowers, which have been drawn from nature by E. Heyn at my request, and reproduced in the accompanying Plate XII. entitled "Alpine Flowers in the Tyrol," it will be seen at once that every colour is to be met with here. White and red, yellow and blue, brown and green stand in varied combination side by side on a hand's-breadth of space. The bees, humble-bees, flies, and butterflies which are dependent on the honey and pollen of these flowers may also be seen in Alpine regions flying about at this same time. If one of these animals should be late, its existence is endangered on account of the briefness of the period of vegetation, for should it not happen that some belated flower blossoms in a hollow where the high-piled winter snow has lingered for a long time, the animal is in imminent risk of perishing from lack of food.

THE SCENT OF FLOWERS CONSIDERED AS A MEANS OF ATTRACTING ANIMALS.

The scents of flowers, like their colours, are very intimately connected with the Animal Kingdom. The scent of foliage, stems, and roots, as mentioned elsewhere (vol. i. p. 431), serves very efficiently to frighten and ward off herbivorous animals; but the scent emitted from the flowers, on the other hand, serves to allure such animals as transfer the pollen from flower to flower and from plant to plant


Pedicularis Oderi
Gentiana Clusii
Gentiana verna
Silene acaulis
Androsace obtusifolia
Saxifraga caesia
Carex firma



ALPINE FLOWERS IN THE TYROL.

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by their visits, thus rendering them an important service. In the Auricula (*Primula Auricula*), Woodruff (*Asperula odorata*), Rue (*Ruta graveolens*), and Lavender (*Lavandula vera*), the flowers and foliage have the same scent, and here the insects seeking for honey and pollen are allured to the flowers, whilst the flowers and foliage are protected from being devoured by grazing animals by one and the same substance. A uniform distribution of odorous substance over different parts of the same plant is, however, comparatively rare; much oftener the scent of the flowers differs from that of the foliage. Thus the Garlics (*Allium Chamæmoly, Sibiricum, suaveolens*) develop the scent of honey in their flowers which brings insects to visit them, while their leaves have a strong odour of onions which keeps grazing animals at bay. In most Umbelliferæ the flowers have a different scent from the foliage-leaves, stem, and roots. The leaves of the Umbelliferous *Euryangium sumbul* (mentioned on p. 745, vol. i.) smell of musk, the root of the Coriander (*Coriandrum sativum*) gives off an offensive odour of bugs, and the Common Hemlock (*Conium maculatum*) has a repulsive odour of mice. And yet the flowers of these three Umbellifers all have a delicate scent of honey, which allures insects to visit them.

The number of scents is very great. At least five hundred can be distinguished. On attempting to classify them and to state their qualities one meets with a serious difficulty, for language is not rich enough to give names to all the different kinds, and nothing remains but to say that Mignonette flowers have a Mignonette scent, Rue flowers have the scent of Rue, and so forth. The need of bringing this multiplicity into something like order, of placing similar scents together and fixing on a central point round which the others could be grouped, as has been done with the ground tints and ground colours, has long been felt, but hitherto sufficient attention could not be given to the need, because the chemical properties of scents which must serve as the basis for any scientific division are only very imperfectly known. However, in what follows the classification of scents which is attempted does not pretend to completeness nor to infallibility, but is to be regarded solely as a first attempt or preliminary outline to which one can turn provisionally in the naming these scents.

Five groups of floral scents may be conveniently distinguished, *i.e.* the indoloid, aminoid, paraffinoid, benzoloid, and terpenoid scents.

To the first group, the *indoloid* scents, belong those volatile substances which arise from the decomposition of albuminous compounds and diffuse into the atmosphere, and in which one or several benzole nuclei are retained, as well as nitrogen; examples are Leucin and Tyrosin, Skatol and Indol. The group derives its name from the last-named substance. These are developed in the inflorescences of numerous Aroids, in the flowers of all the South African Stapelias, in those of the Balanophoreæ, Rafflesiaceæ, and Hydnoreæ, in the perianths of about 200 Aristolochias, and also in those of some tropical Orchids, as, *e.g.* of *Bolbophyllum Beccarii* of the Malayan flora. Sometimes the scent resembles that of decomposing mammalian flesh, sometimes of rotten fish (*cf.* vol. i. p. 196), sometimes again of decomposing animal excreta. The West Indian *Aristolochia Gigas* has the scent of old decaying tobacco, and the red-brown flowers of *Calycanthus* smell like fermenting wine, quite unlike the woody branches, which have a pleasant odour reminding one of cloves. It has already been stated that flowers provided with indoloid scents resemble animal corpses in their colouring, having usually livid spots, violet streaks, and red-brown veins on a greenish or fawn-coloured background.

The *aminoid* scents come next to the indoloid. Under this name are comprised all those volatile substances which diffuse into the air and have an amine as their foundation, either a primary, secondary, or tertiary amine, according as to whether one, two, or all three of the hydrogen atoms of the ammonia are replaced by an alcohol radical. It has been shown that the curious odour of the Hawthorn (*Cratægus*) is due to trimethylamine. It is very probable that in numerous other flowers with similar scent trimethylamine or a related compound—ammonia—is developed. The smell of Hawthorn flowers is repeated with slight modifications in the flower of the Pear (*Pyrus*), the Medlar (*Mespilus*), the Mountain Ash (*Sorbus*), the shrubby Spiræas (*Spiræa ulmifolia, chamædryfolia*, &c.), the Dogwood (*Cornus sanguinea*), the Wayfaring Tree and Guelder-rose (*Viburnum Lantana, Opulus*), the Chestnut (*Castanea*), the Elder (*Sambucus racemosa*), the Traveller's Joy (*Clematis Vitalba*), and the Barberry (*Berberis*). The scent which is liberated from the flowers of the Tree of Heaven (*Ailanthus*), of the Horse-chestnut (*Æsculus Hippocastanum*), of the Flowering Ash (*Fraxinus Ornus*), and of the Evening Primrose (*Œnothera*), resembles that of *Cratægus* more remotely. The flowers of the Ivy (*Hedera*) develop a scent which reminds one of herring-pickle, those of the Alpine Poppy (*Papaver alpinum*), partly of Hawthorn, partly of Musk. Two North American plants, viz. *Pachysandra* and *Sanguinaria*, produce a scent distantly resembling ammonia which proceeds, apparently, from an amine compound. Under this division, finally, should be placed that odour so repulsive to the human olfactory organ which is produced by the flowers of the already-mentioned *Melianthus* (see p. 171).

The third group, that of the *benzoloid* scents, is composed of such as are formed from the so-called aromatic bodies. They are compounds with a benzole nucleus in which the various hydrogens of the benzole are replaced by alcohol and acid radicals. The Eugenol (or oil of cloves) in the flowers of many Pinks (*Dianthus Caryophyllus, plumarius, superbus*), the Cinnamyl-alcohol which smells like Hyacinths, the Salicylic aldehyde in the flowers of the Meadow-sweet (*Spiræa Ulmaria*), the Coumarin in the flowers of the Woodruff (*Asperula odorata*), the Vanilla-like scent in the flowers of the Heliotrope (*Heliotropium*) are all well-known chemical compounds. I would also include with these the scents of the Lilac (*Syringa vulgaris*), Lily of the Valley (*Convallaria majalis*), Mignonette (*Reseda odorata*), Jessamine (*Jasminum officinale*), Auricula (*Primula Auricula*), Honeysuckle (*Lonicera Caprifolium*), Acacia (*Robinia Pseudacacia*), Violet (*Viola odorata*), Cyclamen (*Cyclamen Europæum*), Paulownia (*Paulownia imperialis*), and of Ilang-Ilang (*Cananga odorata*).

It is very remarkable that many of these benzoloid scents are repeated in species of very different plant-families. Clove-scent is apparent not only in the above-named Pinks but also in the flowers of many species of Broom-rape (*Orobanche caryophyllacea, gracilis, lucorum*), in some Orchids (e.g. *Habenaria bifolia, Gymnadenia conopsea*), in the yellow flowers of *Ribes aureum*, in the Narcissus (*Narcissus poeticus*), and in a somewhat modified form in the flowers of *Azalea pontica.* Many Catchflies (*Silene nutans, longiflora,* &c.), the Dame's Violet (*Hesperis tristis*), and the dark-flowered Pelargoniums (*Pelargonium atrum, glaucifolium, triste,* &c.) develop the scent of Hyacinth flowers. It has long been known that the scent of Woodruff is found in the flowers of many Grasses (*Anthoxanthum, Hierochloe*), and mixed with honey-scent in the flowers of the Melilot (*Melilotus*). The scent of Vanilla is very widely distributed. Besides the Heliotrope (*Heliotropium Europæum* and *Peruvianum*) some species of Woodruff (e.g. *Asperula glomerata, cynanchica, longiflora*), the Linnæa (*Linnæa borealis*), the Dwarf Elder (*Sambucus Ebulus*), the small Bindweed (*Convolvulus arvensis*), some Orchids of our upland and alpine meadows (e.g. *Gymnadenia odoratissima, Nigritella nigra*), the alpine Saussurea (*Saussurea alpina*), the alpine Spurge Laurel (*Daphne alpina*), and the Nardosmia (*Nardosmia fragrans*) are provided with vanilla-scent to a greater or less degree. Different, but still resembling Vanilla, is the scent of tropical Orchids of the genus *Stanhopea*, and the exactly similar scent of *Epipogium aphyllum*, which grows in European Pine-forests. Lilac scent is less common, but it is found clearly enough in many allies of the Spurge Laurel (e.g. *Daphne striata* and *pontica*). This is the more strange, since the flowers of these Daphnes, though not even related to the Lilac, resemble Lilac flowers to a surprising extent at first sight. On the other hand, many species of the genus *Syringa*, e.g. *Syringa Emodi*, which grows on the Himalayas, have a scent which differs from that of *Syringa vulgaris* (the Lilac). The Lily of the Valley scent is on the whole rarely met with—only in some Mexican Cactuses, especially in *Echinocactus Tetani.* Acacia scent is found in a good many Papilionaceæ, as, for example, in *Cladrastis lutea, Cytisus alpinus*, and *Spartium junceum*, and also in the flowers of an Iris (*Iris odoratissima*). Auricula scent, besides in many Primulas allied to *Primula Auricula*, is present in the flowers of the Globe-flower (*Trollius Europæus*). Honeysuckle scent is emitted in the evening from the flowers of all the species allied to *Lonicera Caprifolium*, and also in the flowers of *Ismene*, and of a species of Tobacco (*Nicotiana affinis*). Violet scent is fairly widely distributed. In addition to numerous species of Violet (e.g. *Viola odorata, mirabilis, polychroma*) it is also developed in many Cruciferæ, thus, in the Stocks (*Matthiola annua, incana, varia,* &c.), in the Wallflower (*Cheiranthus Cheiri*), and in the common Dame's Violet (*Hesperis matronalis*). The Snowflake (*Leucojum vernum*), the autumn-flowering fringed Gentian (*Gentiana ciliata*), the Spurge Laurel (*Daphne Laureola* and *Philippi*), the blue Water-lily of the Nile (*Nymphæa cærulea*), and the insectivorous Sarracenia (*Sarracenia purpurea*) emit an unmistakable scent of Violets from their flowers. Cyclamen scent is again found in the flowers of a Winter-green (*Pyrola uniflora*); *Paulownia* scent in the flowers of *Glycine Chinensis*; and Unona scent in the flowers of *Zaluzianskia lychnidea*.

The acids and alcohols of those hydrocarbons which are known as paraffins differ chemically from the benzoloid scents. The name *paraffinoid* may be given to them. With regard to their composition the best known of these compounds are Valerianic acid yielded by the Valerian scent in the flowers of numerous Valerians, especially of *Valeriana officinalis, montana,* and *saxatilis*; Pelargonic acid, which is closely connected with Rose scents, and especially with that of *Rosa centifolia*; the Oil of Rue which is liberated from the flowers of various Rutaceæ, especially of the Common Rue (*Ruta graveolens*); and the volatile Œnanthic acid which is met with as the wine-flower scent in the flowers of the Vine (*Vitis vinifera*), and of Gleditschias (*Gleditschia triacanthos, Sinensis,* &c.). To this group belong also the Lime scent which diffuses with various modifications from the flowers of different Limes (*Tilia alba, Americana, parvifolia,* &c.), and also from those of *Æsculus macrostachya*; the very widely-distributed Nightshade scent from the flowers of many species of the Thorn-apple (*Datura*), of the Mandrake (*Mandragora*), the *Petunia* and numerous other Solanaceæ, as also from those of the Peony (*Pæonia*), and American *Trillium grandiflorum*. The Elder scent of the flowers of *Sambucus nigra* and *Orchis pallens*, and the hircine odour, resembling caproic acid, which is liberated from the flowers of the Lizard orchis (*Orchis hircina*), and, somewhat modified, from those of *Orchis fragrans* are also to be included.

It is uncertain whether the honey scent of fresh yellow bees'-wax and honey developed in so many flowers belongs to the paraffinoid series or not. Formerly it was thought that myricilalcohol (an alcohol of paraffin) caused this peculiar scent. But it would appear that the purified myricilalcohol is scentless, so that it is therefore possible that the honey scent is due to another compound. At any rate, it is naturally associated with the above-mentioned scents, and can be most conveniently described here. It is a very common, if not the commonest of all flower scents. The fact that it is often combined with others, especially with benzoloids, leads to the formation of many varieties. The scent, which is most like that of honey-filled honey-comb fresh from the hive, is produced by the flowers of the Sloe, Apricot, Cherry, and Almond trees (*Prunus spinosa, Armeniaca, avium, Amygdalus communis,* &c.), of *Herminium*, belonging to the Orchids, of the Buckthorn (*Rhamnus pumila,* &c.), and of the Bugwort (*Cimicifuga fœtida*). A slightly different scent is liberated by the flowers of the Bird Cherry (*Prunus Padus*), the Bedstraws (*Galium Cruciata, vernum, verum*), of the alpine Forget-me-not (*Myosotis alpestris*), and Phlox (*Phlox paniculata*), of *Asclepias* and *Cynanchum*, the Corydalis (*Corydalis cava*), many species of Spurge (*Euphorbia Cyparissias,* &c.), the Willows (*Salix Caprea, daphnoides,* &c.), some Compositæ (e.g. *Cirsium arvense* and *brachycephalum*), numerous Umbelliferæ (e.g. *Angelica officinalis, Heracleum Sphondylium, Meum Mutellina, Pimpinella magna*), many Cruciferæ (e.g. *Alyssum montanum, Erysimum odoratum*), many Tulips and

Garlics (*Tulipa sylvestris, Allium Sibiricum, Chamæmoly,* &c.), of the Buckwheat (*Polygonum Fagopyrum*), and of many others. The sweet scent of the Clover which occurs in species other than the common meadow Clover (*Trifolium pratense*) and in other Papilionaceæ (e.g. *Trifolium resupinatum, Lathyrus odoratus*) is only a form of honey-scent.

The last group consists of scents produced from ethereal oils destitute of oxygen called terpenes; the scents corresponding to them may therefore be called *terpenoids.* The materials which give rise to these scents are found sometimes in special receptacles imbedded in the plant-tissues, sometimes in the enlarged end-cells of the so-called glandular or capitate hairs—for the most part in the region of the stem and foliage, more rarely in the flowers. The best-known terpenoid scent occurring in flowers is that of the Orange-flower, produced by Oil of Neroli, which is obtained by distillation of the flowers of *Citrus Aurantium*; in those of Gardenias (*Gardenia*), of *Pittosporum Tobira,* of the Siberian *Pyrus baccata,* and somewhat modified in the flowers of some Magnolias (e.g. *Magnolia obovata* and *Yulan*); also the Citron scent from Oil of Citron which occurs in the flowers of some species of Thyme (*Thymus citriodorus, montanus,* &c.), more especially in those of Fraxinella (*Dictamnus Fraxinella*), and the scent of Lavender which is produced from the Oil of Lavender present not only in the foliage but also in the flowers of *Lavandula.*

It has already been incidentally mentioned that two kinds of scent are often liberated simultaneously from the same flower, and that the scent of honey, in particular, frequently combines with some other. The identification of the scent is rendered much more difficult under these circumstances, especially as sometimes one, sometimes the other scent predominates according to the time of day. Not unfrequently one hears wholly different opinions about the scent of a flower. One observer thinks it to be vanilla, perhaps, another a violet scent. Both may be right, since two kinds of scent may be actually liberated from the same flower, whilst individuals are frequently unequally susceptible to all odours.

The difficulties of identifying the flower scent are also increased by the fact that a certain amount of imagination is almost unavoidable. Taste and sight may also be at fault. On looking at a Carnation one is immediately reminded of the smell of cloves before the scent has actually reached the nose. It is therefore advisable that the flowers should not be seen while their scent is being identified, and that to examine them one should get a friend to hold them before one's nose after one's eyes are shut.

It is noticeable that similar and closely-allied species of plants often have different scents. Many examples have already been given, amongst others that *Gymnadenia conopsea* has the smell of cloves, and the very similar *Gymnadenia odoratissima* a vanilla scent. Of species of the genus *Daphne, Daphne alpina* has a vanilla scent, *Daphne striata* a lilac scent, *Daphne Philippi* a scent of violets, and *Daphne Blagayana* a clove scent. The closely-allied *Orchis fragrans* and *coriophora* can be at once distinguished by the smell of their flowers. The scents occurring in different species of *Syringa, Tilia,* and *Sambucus* can also be easily recognized. In Roses this phenomenon is even more remarkable. From their scents *Rosa alpina, pimpinellifolia, arvensis, Indica, moschata, canina, Gallica, cinnamomea, Centifolia,* and *Thea* can be at once distinguished with closed eyes by anyone who has examined the numerous species of this genus even to a limited extent. It is also remarkable that in closely-allied species the flowers of one will smell while those of another will be scentless. *Habenaria montana* has no scent, whilst *Habenaria bifolia* exhales a strong scent of cloves. *Viola tricolor* is scentless, *Viola polychroma* develops a strong violet scent. The flowers of *Primula Lehmanni* have no scent, while those of *Primula Auricula,* which can hardly be distinguished from the former, have a strong Auricula smell. These facts are not without bearing in the theory of specific constitution of protoplasm, as will be discussed later on in the chapter on the Origin of Species, and therefore should be noted here in passing.

We are liable to many erroneous inferences with regard to the perception of flower scent by animals, since our judgment depends mainly on our own sense of smell, and it is very possible, even probable, that the power of smell in flower-visiting animals differs materially from ours. The olfactory sense of man is lodged in a sharply-defined portion of mucous membrane in the upper part of the nasal cavity. There the superficial cells of the mucous membrane join with the end branches of the olfactory nerve in a peculiar net-work, and the scents must act directly on this region if they are to produce the sensation of smell. But this is again only possible if the odorous substances give off fine particles into the air, and if this impregnated air is wafted over the special part of the nasal mucous membrane. It was formerly held that the substances passing thus over the olfactory mucous membrane were dissolved in a fluid and were then distributed in solution. Only in this way could they influence the nerve-endings. But this view is contradicted by a series of facts of which the most important are the following: it is well known that we can smell certain metals whose finely-divided particles break away and enter the nose, although these metals are certainly not soluble in the mucous membrane. We are also able to smell very different scents quickly, one after the other, which would not be the case if the sense of smell were dependent on a previous solution of the odorous substance in the fluid which saturates the mucous membrane. Again it is a remarkable fact that the mucous membrane is altogether absent from the olfactory organ of many animals. The knobs and pegs on the surface of the feelers which form the olfactory organs of insects are indeed connected on one side with gangliose nerve-endings, but they have nothing resembling a mucous membrane which could contain or secrete a fluid, and yet insects are characterized by their fine sense of smell.

The stimulation of the nerve-endings in the olfactory organ cannot therefore be the result of a previous solution of the odoriferous substance, but must be considered as the transference of a movement. It seems as if the molecules of the odorous substance which are present in the air undergo a rotatory, vibrating, or some kind of swinging movement, and that this movement is transferred to the nerve-endings as soon as the molecules come into contact with the olfactory organ. Since the nerve-endings are not exposed the transference must take place through the portion overlying the nerve-ends, and it must depend upon the structure of this superficial layer which is exposed to the air whether the transference takes place quickly or slowly, completely or only partially. It is necessary that the stimulation of the nerve-endings, which we imagine to be a form of movement, should be conducted to the central organ if it is to be perceived as smell. But now arises this difficult question: Do the various sensations of smell depend upon the fact that different nerve-endings are stimulated by different odorous substances, and that a particular scent, *e.g.* that of Oil of Lavender, is only perceived when those particular nerve-ends are stimulated which are sensitive to the kind of vibration undergone by the molecules of the Oil of Lavender? Or, are they caused directly by the movement of the molecules of any odorous substance being transmitted by any olfactory nerve-fibre to the central organ, and there producing a definite sense of smell? In this case the same nerve-fibre which had just transmitted the vibrations of the lavender oil would be capable in the next moment of transferring to the central organ those belonging to the molecules of chloroform.

The one hypothesis assumes that certain parts of the central organ, as well as the nerve-fibres leading to them, differ essentially from one another in their capability of being stimulated, although they seem to our senses to be of exactly the same structure. One part can only be stimulated by Oil of Lavender and is not affected by chloroform molecules, another part is only set into a corresponding movement by the swinging of chloroform molecules, but is not in sympathy with the particular movement of those of lavender oil. But to favour this hypothesis is to assume an enormously large number of different nerve-endings in the olfactory organ considering the innumerable quantity of different odoriferous substances that exist—even if it be granted that there is a place only for groups of similar substances in the olfactory organ and not for each singly, the individual scents of each group being only produced by the different degree of the stimulation. The other hypothesis assumes that each olfactory nerve-fibre according to its structure is enabled to transmit the different forms of movement which occur at its peripheral end to the central organ. The particular movements of the molecules of lavender oil would not only affect the nerve-ends, but would continue as a specific form of movement through the whole nerve-fibre to the central organ, and would be there perceived as the scent of lavender oil. This same nerve-fibre which had just transmitted the scent of lavender might in the next moment transmit the vibrations of chloroform and produce the chloroform smell. Such conduction resembles that of a telephone at least in this that different words spoken at one end through the same telephone can be heard unaltered at the other end. The assumption of a conduction of specific forms of movement set up by odorous substances from the periphery through the whole nerve-fibre up to the central organ, also renders it necessary to assume that the olfactory nerve-fibres are not stimulated at all by certain materials. Thus vibrations which exceed the limits of irritability of the olfactory nerves in rapidity produce no smell.

Whichever hypothesis one accepts one comes to the conclusion that a great difference may exist between the sense of smell of men and animals according to the different degree of sensitiveness of their olfactory fibres. Although the molecules of a substance floating in the air stimulate (*i.e.* set in motion) no single nerve-ending in the human olfactory mucous membrane, this does not prove the absence of nerves in the olfactory organ of some animal sensitive to the particular form of motion of these molecules. It might easily happen that one insect would smell Hyacinths but not Roses, while another would smell Roses and not Hyacinths. This conclusion is, however, of importance in explaining the allurement of certain animals to flowers which appear scentless to man, as well as in explaining the phenomenon that many flowers are eagerly visited by one group of insects and are avoided or rather ignored by another. The Virginian Creeper, *Ampelopsis quinquefolia*, so often planted to cover porches, palings, and walls, develops flowers in midsummer which are visited by bees very industriously and eagerly. The colour does not act as an allurement in this case, for the flowers have green corollas, are hidden away under the foliage, and cannot be seen even by good eyes at a little distance. Yet the bees fly thither from all sides in such a way as to leave no doubt that the flowers of the *Ampelopsis* can be perceived by them a considerable way off. Since it is not their appearance it must be their smell which announces their presence! But to men they appear to be quite scentless! The flowers of the Common Bryony (*Bryonia dioica*) are not less remarkable. They occur on two kinds of plants, *i.e.* on one plant are developed only staminate and on the other only pistillate flowers, and since the pollen is not powdery, and therefore not scattered by wind, it must be carried by insects from plant to plant if the ovules are to mature. But the flowers, especially the pistillate ones, are very insignificant, green in colour, with faint smell, and they are half hidden under the foliage. Many insects fly past them without noticing them. They are almost exclusively visited by one of the Hymenoptera, viz. *Andrena florea*, and it can find them even in the most out-of-the-way places. This can hardly be accounted for except by supposing that the scent of Bryony flowers is perceived by these particular bees and not by other insects. To these two examples of insignificant flowers, which appear to men and to many animals to be scentless but which are nevertheless eagerly tracked by certain insects, may be added the common Birthwort (*Aristolochia Clematitis*), the Whortleberry (*Vaccinium Myrtillus*), *Chamæorchis alpina*, the Twayblade (*Listera ovata*), and many others. It is probable that there are also flowers which differ from these in having bright colours contrasting with the green foliage, and in addition exhale a special scent to allure certain animals. It is, of course, hardly possible to speak with certainty. In all these questions we have to deal with observations concerning the relations between insects and flowers in nature, and since many sources of error exist, the conclusions arrived at must be accepted with discretion. As to the so-called "flower fidelity" of insects, by which is meant the preference of certain kinds for certain flowers, the matter is only mentioned here very generally so far as the scents are concerned, and only the main results of these observations are given.

It may be stated as one of these that the indoloid scents have an attraction for certain flies of the genera *Scatophaga, Sarcophaga, Onesia, Lucilia, Pyrellia, Calliphora, Sepsis,* and *Musca,* and for beetles of the genera *Aleochara, Dermestes,* and *Saprinus,* which appear on carrion and excrement; indoloid scents remain unnoticed, on the other hand, by butterflies, bees, and humble-bees. Aminoid scents attract large and small beetles, especially Cetonias, and after them Hymenoptera; butterflies, however, are hardly ever allured by them. The scent of honey acts powerfully on bees and humble-bees; also on butterflies, burnet-moths (*Zygæna*), and on day-flying hawk-moths (*e.g.* the Humming-bird Hawk-moth, *Macroglossa stellatarum*), as well as on small beetles; but insects which are attracted by indoloid scents are not affected by the scent of honey. Certain Hymenoptera which, oddly enough, themselves have paraffinoid scents (viz. species of *Prosopis*), fly to flowers with the same smell. Flowers with the scent of Honeysuckle are frequented by large crepuscular hawk-moths, but this scent has no attraction for beetles. Butterflies will pass over flowers with a Honeysuckle scent without pausing, leading us to think that either the scent is not perceived by them, or that they find it unpleasant.

Many flower scents, especially the paraffinoids, are less easily perceived at their place of origin than at a little distance, which is explained by supposing that the odorous particles liberated from the flowers are acted on by oxygen or aqueous vapour as they diffuse through the air, and that various molecular changes go on in them. But since our knowledge of the chemical properties of scents is still so imperfect we must beware of suppositions of this kind. The phenomenon is most pronounced in the Lime and in the Vine. As one approaches a Lime-tree in full flower the pleasant scent of its blossom is strongest at a distance of about 30 yards; if one comes into the immediate neighbourhood and smells the flowers on its lower branches, the scent is neither so strong nor so pleasant as it was further off. In a journey up the Danube, through the part of the valley called the Wachau, with its Vine-clad slopes, I found the air of the whole valley, even that above the water, so filled with the scent of Vine flowers that it seemed almost impossible they should be so far off. And yet the nearest Vines on the banks were 100 yards above the water, and at least 300 yards from the boat. Afterwards I found when wandering through the vineyards that the smell of the flowers close at hand was much weaker than at a distance, and was forced to the paradoxical opinion that with increasing distance and diffusion over a wider area the scent does not diminish but waxes stronger.

The fact that man can perceive certain odoriferous substances in the finest state of division and at incredible distances paves the way for explaining the so-called animal perception of scents. We speak of this animal perception when we gather from other signs that an animal is able to smell what we cannot at the same distance. Since it has been already explained that animals can perceive scents which will not stimulate our olfactory nerves at all, it is not wonderful that bees will fly from a distance to the flowers of *Ampelopsis*, although they are not able to see these flowers so far away. They smell the flowers of *Ampelopsis* which are scentless to us at 300 yards, just as we do the flowers of the Vine at the same distance.

Of the multitude of remarkable observations concerning the power of smell in animals only those interest us here which are connected with the visits of insects to flowers; of these, two deserve special mention. Some years ago the Aroid *Dracunculus Creticus* from Cyprus was planted on the edge of a small group of coniferous plants in the Vienna Botanic Gardens. There was no dungheap or decomposing animal matter anywhere in the vicinity, nor was there any trace of carrion-flies or beetles. But when during the summer the large cornet-shaped flower-sheath of this Aroid opened, innumerable carrion-flies and dung-beetles flew thither at once from all sides. The indoloid scent emanating from the flower-sheath was only noticeable by human beings a few yards off, but the animals named must have smelt it many hundred yards away. In a certain part of this same garden there is a plant of Honeysuckle (*Lonicera Caprifolium*), and in summer when twilight falls this is regularly visited by the Convolvulus Hawk-moth (*Sphinx Convolvuli*). These hawk-moths are accustomed, after they have sucked the honey and when the twilight fades into night, to settle near the plant on the bark of old tree-trunks or on fallen leaves, and there they remain with folded wings as if they were benumbed until the next evening. A few summers ago I very carefully picked up one of the pieces of wood which had been chosen as a resting-place by one of these hawk-moths. I marked the moth slightly with cinnabar and brought it, together with the piece of wood on which it remained immovable, to another part of the gardens 300 yards away from the Honeysuckle. When twilight fell the hawk-moth began to wave the feelers which serve it as olfactory organs hither and thither a few times, then stretched its wings and flew like an arrow through the garden towards the Honeysuckle. Shortly after I met the hawk-moth with the cinnabar mark hovering over these flowers and sucking the honey. It had flown straight to the plant, and must have been able to smell the scent of the flowers even at so great a distance.

One of the most remarkable correlations between flower scent and animals is the development of the scent simultaneously with the time of flying of certain insects. The flowers of certain species of Honeysuckle, which are much visited by crepuscular Lepidoptera (*Lonicera Caprifolium, Periclymenum, Etrusca, grata*, &c.), of Petunias (*Petunia violacea, viscosa*, &c.), of *Habenaria bifolia*, and of many other plants, smell very faintly or not at all through the day. After sunset, from about 6 or 7 in the evening until midnight, they give off an abundant odour. Still stranger is the behaviour of the flowers of *Hesperis tristis*, of the dark-flowered Pelargoniums (*Pelargonium triste, atrum*, &c.), and of numerous Caryophyllaceous plants (*Silene longiflora, nutans, viridiflora*, &c.), which are visited by small nocturnal moths, and give off no scent during the day, but exhale a strong Hyacinth odour at twilight. Similarly the flowers of the common Dame's Violet (*Hesperis matronalis*) smell like Violets in the evening, and those of a species of Woodruff (*Asperula capitata*) smell of vanilla as darkness approaches. On the other hand, many flowers visited during the day by butterflies, bees, and humble-bees become scentless at sunset. The yellow flowers of *Spartium scoparium* only exhale their exquisite acacia scent when the sun is high and the insects named are swarming through the warm air. In the evening there is no trace of the scent. The ornamental Clover, *Trifolium resupinatum*, whose flowers are surrounded by bees, smell strongly of honey in the sunshine, but become scentless as soon as the bees return to their hive at twilight. The same is true of the Grass of Parnassus (*Parnassia palustris*), which only smells of honey in bright sunshine and becomes scentless in the evening. A species of Daphne growing in the Pyrenees (*Daphne Philippi*) liberates a delicate scent of Violets during the day, only ceasing to smell when night falls.

It is sometimes suggested that colour and scent in flowers to some extent mutually exclude one another, so that in cases where the allurement of honey- and pollen-eating insects is brought about by the bright colour of the corolla, the scent is absent, and *vice versa*. This idea is supported by the facts that many flowers with brilliant colouring, which can easily be seen at a distance on account of their large size, have no scent, *e.g.* the flowers of the Cornflower (*Centaurea Cyanus*), the Pheasant's Eye (*Adonis æstivalis* and *flammea*), many Gentians (*Gentiana acaulis, Bavarica, verna*), various species of Lousewort (*Pedicularis incarnata, rostrata,* &c.), the Camellia (*Camellia Japonica*), the Indian Azalea (*Azalea Indica*), and numerous species of *Amaryllis* and *Hemerocallis*; whilst, on the other hand, many plants with small and insignificant flowers, as, for example, the Mignonette (*Reseda odorata*), the Vine (*Vitis vinifera*), the Ivy (*Hedera Helix*), Gleditschia (*Gleditschia triacanthos*), and Eleagnus (*Eleagnus angustifolia*) give off a strong scent which can be perceived at some distance. It might be also pointed out that the oft-mentioned Pelargoniums (*Pelargonium atrum* and *triste*) and *Hesperis tristis*, which bear dirty yellow and dark flowers, indistinguishable to the best sight in twilight, develop a strong Hyacinth odour, which allures numerous small night-flying Lepidoptera. But however conclusive these examples may be, there are many others of the opposite kind, *i.e.* of bright and noticeable colours, occurring not infrequently in conjunction with strong scents. Roses, Pinks, and Stocks, many tropical Orchids, Magnolias, Narcissi and the large-flowered Rhododendrons of the Himalayas show at least that the view mentioned has not a universal application.

OPENING OF THE PASSAGE TO THE INTERIOR OF THE FLOWER.

The removal and transmission of pollen by animals can obviously only take place when the perianth-leaves, under whose protection the pollen and stigmas are matured, permit of access to the base of the flower. I have altered the usual expression "Opening of Flowers" in the headline above, since flowers exist to which the term "open" does not apply. The flowers of the Snapdragon and Toadflax (*Antirrhinum* and *Linaria*) never open spontaneously; but the insects which frequent them for honey have to open the door for themselves by pushing down the lower lip. So, also, in the flowers of Papilionaceæ. In the bud the uppermost petal or standard incloses the four others like a mantle; only when the pollen is mature, and has been discharged from the anthers, does the standard fold back, and one says the plant is in flower. But still no opening is to be seen, access to the honey remains now, as before, hidden, and insects must introduce their probosces between the folded petals. Still, from a consideration of these and other cases, it may be urged that there is essentially an opening of what was closed in the bud, a giving of access to the interior of the flower, so that perhaps the headline above meets the case.

The arrangement of the petals in the flower-bud is determinate for individual cases, and is often made use of by descriptive botanists as a useful character for discriminating families and genera. This manner of folding is known as *Æstivation*, of which several forms are distinguished. (1) The *crumpled* æstivation, characteristic of the Poppy, Cistus, and Pomegranate (*Papaver*, *Cistus*, and *Punica*). The petals here, to quote Grew, "are cramb'd up within the *Empalement* [*i.e.* calyx] by hundreds of little *Wrinkles* or *Puckers*; as if Three or Four fine *Cambrick Hankcherchifs* were thrust into ones *Pocket*". (2) *Plaited* or *plicate* æstivation, where a funnel- or bell-shaped corolla is folded in regular, longitudinal pleats, as in Venus's Looking-glass (*Specularia*). (3) When the band-like corollas of many Composites, as the Salsify and Dandelion (*Tragopogon* and *Taraxacum*) are rolled up longitudinally into a tube closed above by five little teeth, one speaks of a *convolute* æstivation; (4) when, as in Umbelliferæ and many Caryophyllaceæ, the petals are rolled up from apex to base, of a *circinate* æstivation. (5) Sometimes the folded or unfolded petals are so placed one upon the other, that on one side each is in contact with the adjacent petal of that side, and on the other side with that of the other, the whole corolla appearing spirally twisted. This condition is known as *contorted* æstivation, of which examples are the Wood-sorrel (*Oxalis*), Periwinkle (*Vinca*), and other Apocynaceæ, Solanaceæ, and Convolvulaceæ. (6) The commonest form of æstivation is that in which the petals or lobes of a united corolla overlap like tiles on a roof, without being twisted, however. The outmost petal covers all the rest, or a pair of outer petals inclose a pair of inner ones. This, the *imbricate* æstivation, is characteristic of the Apple, Rose, Buttercup, and Anemone, also, in a modified form, of Papilionaceæ and Pinks. (7) In a number of plants, e.g. *Asarum*, Lilac, and Vine, the petals do not overlap, but touch merely by their margins, and form a sort of dome or vault. This is known as *valvate* æstivation. Among these kinds of æstivation various combinations occur, thus the Poppy in addition to being crumpled is imbricate, and several Pinks (*Dianthus neglectus*, *glacialis*, &c.) with imbricating petals are also convolute. It further often happens that the leaves of the calyx have an æstivation differing from that of the corolla. Here, again, the Poppy is an instance in point, its calyx is valvate, and its corolla imbricate and crumpled.

In bilabiate corollas, although the individual parts vary a good deal, the imbricate æstivation is constant, though numerous modifications obtain which cannot be described at length here. Two fairly frequent cases, however, must be described, appertaining to the ringent and personate corollas, to be referred to by and by. In the ringent corolla the upwardly-bent median lobe of the lower lip is placed like a lid in front of the corolla-tube, and upon it lie the two lateral lobes of the same lip; these are covered by the downwardly bent upper lip. In the buds of the Germander (*Teucrium*), the middle lobe of the lower lip is bent up to such an extent that it covers over the anthers like a dome, whilst in those of the flowers of the scrophularineous Snapdragon and Toadflax (*Antirrhinum* and *Linaria*) complete closure of the flower is caused by an inflated portion of the lower lip (the so-called palate), this is covered by the upwardly-directed, central lobe of the lower lip, and this again by the two downwardly directed lobes of the upper lip.

All these obstacles, however, to access to the interior of the flower are soon removed. The petals, having served as protective wrappers to the bud, fall away on the opening of the flower in cases where they have no further function to discharge. This condition, truly, is a rare one, but occurs in the Vine (*Vitis*). The petals here are valvate in the bud and form a dome-like covering to the stamens and ovary; they are green in colour, not readily distinguishable from the foliage, and of little value as attractive organs for insects. Under these circumstances it is of advantage that they should be got rid of quickly. This is accomplished as follows. The petals separate from the flower at the base, each rolls up spirally, and they remain hanging together by their apices for a while like a hood, which is ultimately thrown off in consequence of the expansion of the stamens.

This class of opening of flowers is, as stated, rare. In the great majority of cases the petals play a definite part in the later stages of flowering, and are consequently retained. Access to the interior of the flower is brought about by the development between the petals of wide slits as in the Rampion (*Phyteuma*), or, in ordinary cases, by the entire separation of their free ends from one another; the petals, in fact, spread out, and sometimes even become folded back. This separation, of course, corresponds to the position which the petals previously occupied in the bud. Where the æstivation is valvate, the apices of the petals simply fold back like valves; where it is imbricate, the petals become disentangled; where it is plaited or crumpled, the folds or inequalities become smoothed out. Spirally-twisted buds become untwisted, and it may frequently be observed that two or even three different sorts of movement are necessary for a flower to open.

In this way, in many cases, only a somewhat circumscribed opening arises, leading down to the expanded or tubular interior portion of the flower. In others, again, the whole flower opens widely like a cup or saucer, as in Roses, Anemones, and Peonies.

The separation of the petals usually happens very quickly. In the Honeysuckle (*Lonicera Caprifolium*) opening begins with the folding back of the lowest lobe of the corolla, followed by a similar movement of the others, the stamens become liberated and spread like the fingers of a hand. The whole series of movements can be readily followed, and lasts barely two minutes. Still more rapid is the opening of the Evening Primrose (*Œnothera grandiflora*). The petals spring apart quite suddenly and stretch themselves out within half a minute. If ever the term "bursting open" applies to a flower-bud, it does so here. In several tropical Orchids, also, the parts separate quickly enough for the movements to be readily visible. Thus, in the beautiful *Stanhopea tigrina*, the whole process only occupies three minutes. It is worth mentioning, that during the opening of this flower, a distinct noise is heard, not unlike the report caused by the bursting of the inflated calyx of the Bladder-campion.

There are flowers which open so early in the morning that they greet the first rays of the rising sun with fully expanded corollas. That common garden climber, *Ipomœa purpurea*, opens its buds at 4 a.m. Wild Roses, also, open between 4 and 5 a.m. Between 5 and 6 many species of Flax (*Linum perenne* and *Austriacum*) open. Between 6 and 7, Willow-herbs (*Epilobium angustifolium* and *collinum*), between 7 and 8, *Convolvulus arvensis* and *tricolor*. Between 8 and 9, many Gentians, Speedwells, and Wood-sorrels, and the frequently-cultivated Himalayan Cinquefoil (*Potentilla atrosanguinea*). Between 9 and 10 most Tulips and Opuntias open; between 10 and 11, the Centaury (*Erythræa*) and Chaffweed (*Centunculus*). Between 11 and 12, *Potentilla recta*. From noon till evening comes a long interval. No plant is known in our latitude which, under ordinary circumstances, opens during the afternoon. Towards sunset, however, it recommences. About 6 p.m. the Honeysuckle opens, shortly followed by the Evening Primrose and Campion. Between 7 and 8 p.m. *Hesperis matronalis* and *tristis*, the Marvel of Peru (*Mirabilis Jalapa*), a few Catchflies (*Silene noctiflora* and *vespertina*) and several Thorn-apples (*Datura Stramonium*). Between 8 and 9 more Catchflies (*Silene longiflora, Saxifraga, Vallesia*), a Woodruff (*Asperula glomerata*), and a species of Tobacco (*Nicotiana affinis*). Between 9 and 10, the Queen of the Night (*Cereus nycticalus*, represented on Plate VII. opposite page 642, vol. i.) opens.

As it is with the commencement, so is it with the end of flowering; each happens at a definite time, and every flower endures for a determinate period. Flowers which are only open for a single day are termed *ephemeral* flowers. The annexed table shows the hours of opening and closing of a series of ephemeral flowers.

NAME OF PLANT.	OPENS AT	CLOSES AT	NAME OF PLANT.	OPENS AT	CLOSES AT
Allionia violacea	3–4 A.M.	11–12 A.M.	*Portulaca grandiflora*	8–9 A.M.	6–7 P.M.
Roemeria violacea	4–5 "	10–11 "	*Calandrinia compressa*	9–10 "	1–2 "
Cistus Creticus	5–6 "	5–6 P.M.	*Drosera longifolia*	9–10 "	2–3 "
Tradescantia Virginica	5–6 "	4–5 "	*Arenaria rubra*	10–11 "	3–4 "
Iris arenaria	6–7 "	3–4 "	*Portulaca oleracea*	10–11 "	3–4 "
Hemerocallis fulva	6–7 "	8–9 "	*Spergula arvensis*	10–11 "	3–4 "
Convolvulus tricolor	7–8 "	5–6 "	*Sisyrinchium anceps*	11–12 "	4–5 "
Oxalis stricta	8–9 "	3–4 "	*Mirabilis longiflora*	7–8 P.M.	2–3 A.M.
Hibiscus Trionum	8–9 "	11–12 A.M.	*Cereus grandiflorus*	8–9 "	2–3 "
Erodium Cicutarium	8–9 "	4–5 P.M.	*Cereus nycticalus*	9–10 "	2–3 "

The number of hours during which these flowers remain open are as follows:—

	Hours.		Hours.		Hours.
Hibiscus Trionum	3	*Sisyrinchium anceps*	5	*Iris arenaria*	9
Calandrinia compressa	4	*Roemeria violacea*	6	*Convolvulus tricolor*	10
Portulaca oleracea	5	*Oxalis stricta*	7	*Tradescantia Virginica*	10
Drosera longifolia	5	*Mirabilis longiflora*	7	*Portulaca grandiflora*	10
Arenaria rubra	5	*Cereus grandiflorus*	7	*Cistus creticus*	12
Spergula arvensis	5	*Allionia violacea*	8	*Hemerocallis fulva*	14
Cereus nycticalus	5	*Erodium Cicutarium*	8		

From these tables we see that plants with ephemeral flowers may be arranged in two groups; those in which the flowers open between early morning and noon, and those which open at the commencement of twilight or during the night. The latter may be distinguished as "night-flowerers".

Included with the ephemeral flowers are such as open in the evening between seven and eight o'clock, and remain open the whole night and following morning till past midday, or even till evening. For the most part, these close within twenty-four hours of their opening. To these belong several species of Thorn-apple and Evening Primrose, Morina, the Marvel of Peru, and a few Cactuses (*Datura Metel* and *Stramonium*, *Œnothera biennis* and *grandiflora*, *Morina Persica*, *Mirabilis Jalapa*, *Echinocactus Tetani*).

Another series of plants have the peculiarity that their flowers open for the first time during the morning, close at evening, and open again the following morning, but fade or fall during the afternoon of the second day. Examples are many: Papaveraceæ, many species of Flax, the Raspberry, a few Cinquefoils and Cactuses (*Glaucium corniculatum* and *luteum*, *Papaver alpinum*, *Linum tenuifolium*, *Rubus Idæus*, *Potentilla recta*, and *Opuntia nana*).

The duration of flowering (*i.e.* period of persistence of single flowers) in plants which keep open for more than a single day is indicated, for selected examples, in the annexed table:—

2 Days.

Centunculus minimus.
Dianthus prolifer.
Epilobium collinum.
Geranium pratense.
Papaver somniferum.
Potentilla atrosanguinea, &c.
Rosa arvensis, &c.
Saponaria Vaccaria.
Sinapis arvensis.
Veronica aphylla, &c.

3 Days.

Lonicera Caprifolium.
Potentilla formosa.
Agrimonia Eupatorium.
Aphyllanthes monspeliensis.
Galium infestum, &c.
Helianthemum alpestre, &c.

4 Days.

Lychnis diurna.
Sagina saxatilis.
Sedum atratum.
Scilla liliohyacinthus.
Telephium Imperati.
Sanguinaria Canadensis.

5 Days.

Eschscholtzia Californica.
Fritillaria meleagris.
Scilla Sibirica.
Erythræa Centaurium.
Linum viscosum.

6 Days.

Digitalis purpurea.
Erythræa pulchella.
Hemerocallis flava.
Lilium album.
Oxalis lasiandra.

7 Days.

Ranunculus acer, &c.
Pelargonium zonale, &c.

8 Days.

Eranthis hiemalis.
Hepatica triloba.
Parnassia palustris.
Saxifraga bryoides.

10 Days.

Cyclamen Europæum.

12 Days.

Crocus sativus.
Saxifraga Burseriana.

18 Days.
Vaccinium Oxycoccos.

30 Days.
Cattleya labiata.
Vanda cærulea.

40 Days.
Cypripedium insigne.
Odontoglossum (many).

50 Days.
Epidendrum Lindleyanum.
Phalænopsis grandiflora.

60 Days.
Oncidium cruentum.

70 Days.
Cypripedium villosum.

80 Days.
Odontoglossum Rossii.

The duration of flowers varies then, in different species, from three hours to eighty days. These remarkable differences are connected with the amount of pollen produced in the flowers, and with the number of flowers on each plant. They also depend on whether or no the stigma is entirely dependent on insects for pollen. Flowers with numerous stamens and ample pollen, as for instance, Poppies, Cistuses and Portulacas, have but a brief duration, whilst on the other hand, such as have but a single stamen, *e.g.* most Orchids, remain fresh often for weeks. In plants which produce but a single flower throughout the year, as the Snowdrop, the one-flowered Winter-green (*Pyrola uniflora*), Herb Paris and *Trillium*, or at most two or three, as in the Lady's Slipper Orchid (*Cypripedium Calceolus*), and in tropical Orchids of the genera *Oncidium*, *Stanhopea*, and *Cattleya*, the flowers persist fresh and open for long periods. It may happen also that in consequence of unfavourable climatic conditions flowers may be deprived of insect-visits for many days at a time. In the case of flowers so constituted that in the absence of insects no production of seeds is possible, it follows that in some years the whole object of flowering (where but a single or very few flowers are produced) will be jeopardized. It is obviously of advantage to flowers of this kind that they should be able to hold out for a considerable period. The longer they persist the better is their chance of being visited by insects bringing pollen from other plants.

Let us now take the other extreme, a plant producing numerous flowers, one after the other, in the course of a year, flowers which are able in the absence of insects to pollinate themselves. Here the duration of each flower need be only very short. Notwithstanding the short duration of the flowers the plant remains in blossom for weeks or months. The Spiderworts (*Tradescantia crassula*, *Virginica*, &c.) have ephemeral flowers, but they go on producing them for eight weeks, during the whole of which time the plants are daily provided with new ones. The same holds good in most Crucifers, Cistuses, Rock-roses (*Helianthemum*), Droseras, &c. The last-mentioned open their flowers only under very favourable conditions of weather, and then only every other day. At any rate, for *Drosera longifolia* it has been shown that, even in the finest weather, a flower-bud opens on alternate days only. Thus we see that pretty much the same result is accomplished in the two classes; in those plants possessing numerous, ephemeral flowers, and in those with solitary, long-persisting ones.

It has already been explained (p. 107) that in localities where a heavy precipitation of dew obtains, flowers which remain open for long periods are liable to a saturation of their pollen during the night, and that many protective arrangements prevail to minimize this danger. One of the most commonly occurring of these contrivances is the closing of the flowers at night. The petals fold inwards and become furled in the same positions as they occupied in the bud. Indeed, one may say that the flower becomes a bud again. When consistent with the advantages accruing from insect-visits, flowers close in the evening and only open again next day when the danger of wetting by dew is past. In a great number of cases this periodic opening occurs at the same hour as that at which the flower-bud originally opened. Many flowers open but once again, others twice, thrice, or four times on successive days—the Meadow Saffron daily for twelve days. As soon as any particular kind of insect begins to swarm, those flowers, whose structure is adapted to visits from the variety of insect in question, open. Similarly, when the insects retire to rest, the flowers close lest the pollen be exposed to needless danger. In other words, the flowers of many plants *open and close periodically.*

This remarkable phenomenon has for a long time attracted the attention of Botanists, and Linnæus devised his so-called Floral Clock on the basis of his long-continued observations at Upsala. In this he grouped together plants according to the hours at which they opened and closed their flowers, and ascertained, for every hour of the day, what species were doing either the one or the other. Not only were simple, isolated flowers laid under contribution for this purpose, but the complex heads (capitula) of Composites also, since these periodic movements are very conspicuous in them. True, in Composites it is not the petals of a flower which open and shut, but the flowers (florets) of a head; still the cause and effect are here identical with those in ordinary flowers, and Composites were rightly included in the Floral Clock. If the plants which open and close their flowers periodically be cultivated apart, it is possible to determine the time of day by careful observation in this part of the garden. Formerly, the attempt was often made in Botanic Gardens to construct such a Floral Clock, but never with success, because the plants enumerated by Linnæus do not all flower at the same season. Later, when other fields of Botanical activity came into vogue, it was abandoned as a children's game. Consequently the Floral Clock of Linnæus has fallen into oblivion, and the younger generation of Botanists hardly knows its name. For my own part, I am inclined to give this Clock some consideration, as it has a bearing on several important questions in the life of plants. To recall it to memory, it is annexed below in the table which follows. It was constructed for Upsala, 60° north lat.

3–5 A.M.	
Tragopogon pratense	open.
4–5 A.M.	
Cichorium Intybus	,,
Leontodon tuberosum	,,
Picris hieracioides	,,
5 A.M.	
Hemerocallis fulva	,,
Papaver nudicaule	,,
Sonchus oleraceus	,,
5–6 A.M.	
Crepis alpina	open.
Rhagadiolus edulis	,,
Taraxacum officinale	,,
6 A.M.	
Hieracium umbellatum	,,
Hypochæris maculata	,,
6–7 A.M.	
Alyssum utriculatum	,,
Crepis rubra	,,
Hieracium murorum	,,
Hieracium Pilosella	,,
Sonchus arvensis	,,
7 A.M.	
Anthericum ramosum	open.
Calendula pluvialis	,,
Lactuca sativa	,,
Leontodon hastile	,,
Nymphæa alba	,,
Sonchus Lapponicus	,,
7–8 A.M.	
Mesembryanthemum barbatum	,,
Mesembryanthemum linguiforme	,,

8 A.M.
Anagallis arvensis............open.
Dianthus prolifer............ ,,
Hieracium Auricula .... ,,

8–10 A.M.
Taraxacum officinale .... shut.

9 A.M.
Calendula arvensis............open.
Hieracium chondrilloides... ,,

9–10 A.M.
Arenaria rubra .... ,,
Mesembryanthemum crystallinum .... ,,
Tragopogon pratense......... shut.

10 A.M.
Cichorium Intybus............ ,,
Lactuca sativa.................. ,,
Rhagadiolus edulis............ ,,
Sonchus arvensis............... ,,

10–11 A.M.
Mesembryanthemum nodiflorum ....open.

11 A.M.
Crepis alpina.................. shut.

11–12 A.M.
Sonchus oleraceus............. shut.

NOON.
Calendula arvensis .... ,,
Sonchus Lapponicus .... ,,

1 P.M.
Dianthus prolifer............. ,,
Hieracium chondrilloides... ,,

1–2 P.M.
Crepis rubra.................... ,,

2 P.M.
Hieracium Auricula.......... ,,
Hieracium murorum......... ,,
Mesembryanthemum barbatum,,

2–3 P.M.
Arenaria rubra .... ,,

2–4 P.M.
Mesembryanthemum crystallinum .... ,,

3 P.M.
Leontodon hastile .... ,,
Mesembryanthemum linguiforme .... ,,
Mesembryanthemum nodiflorum .... ,,

3–4 P.M.
Anthericum ramosum......... shut.
Calendula pluvialis .... ,,
Hieracium Pilosella .... ,,

4 P.M.
Alyssum utriculatum......... ,,

4–5 P.M.
Hypochœris maculata .... ,,

5 P.M.
Hieracium umbellatum...... ,,
Nyctago hortensis.............open.
Nymphæa alba................ shut.

6 P.M.
Geranium triste................open.

7 P.M.
Papaver nudicaule .... shut.

7–8 P.M.
Hemerocallis fulva............ ,,

9–10 P.M.
Cactus grandiflorus ....open.
Silene noctiflora............... ,,

MIDNIGHT.
Cactus grandiflorus........... shut.

To the above clock, adapted to the latitude of Upsala, I append a second, based on long-continued observations at Innsbruck (47° north lat.), 13° south of Upsala.

4–5 A.M.
Rosa arvensis (June).........open.

5–6 A.M.
Rosa rubiginosa (June)...... ,,
Solanum nigrum (July)...... ,,

6–7 A.M.
Anoda hastata (July)........ ,,
Cichorium Intybus (July)... ,,
Crepis pulchra (July)........ ,,
Dianthus neglectus (July)... ,,
Gallasia villosa (July)...... ,,
Hieracium amplexicaule (July)......................... ,,
Hieracium aurantiacum (July) .... ,,
Lactuca perennis (August).. ,,
Lampsana communis (July) ,,
Linum grandiflorum (July) ,,
Linum viscosum (July)...... ,,
Mulgedium Plumieri (July) ,,
Ranunculus acer (July)...... ,,
Solanum tuberosum (July).. ,,
Sonchus oleraceus (June) ... ,,
Taraxacum officinale (June) ,,
Tragopogon floccosus (July) ,,
Tragopogon orientalis(July) ,,

7–8 A.M.
Campanula Trachelium(July)op'n
Carlina acaulis (August)... ,,
Carlina vulgaris (August).. ,,
Crepis rubra (August)....... ,,
Gentiana acaulis (May)..... ,,
Geranium lucidum (July)... ,,
Gilea tricolor (July)......... ,,
Hedypnois tubiformis (July) ,,
Hieracium Pilosella (July).. ,,
Hypecoum grandiflorum(July).,
Hypochœris maculata (June) ,,
Lactuca muralis (July) ...... ,,
Oxalis Valdiviana (July)... ,,
Sonchus arvensis (August).. ,,
Specularia Speculum (July) ,,
Tolpis barbata (August).... ,,

8–9 A.M.
Adonis vernalis (April)...... ,,
Brassica oleracea (Sept.).... ,,
Diplotaxis tenuifolia (Sept.) ,,
Gentiana asclepiadea (Aug.) ,,
Gentiana cruciata (July)... ,,
Gentiana utriculosa (June). ,,
Geranium columbinum (Aug.) ,,
Helianthemum alpestre (June) ,,
Isopyrum thalictroides (April)op'n
Lactuca sativa (Aug.)........ ,,
Lactuca Scariola (Sept.).... ,,
Mamillaria glochidiata (Aug.) ,,
Nymphæa alba (Aug.)....... ,,
Ornithogalum Narbonense (July)......................... ,,
Oxalis lasiandra (Aug.)..... ,,
Veronica Persica (June).... ,,

9–10 A.M.
Anagallis arvensis (July)... ,,
Anemone Hepatica (April).. ,,
Anemone nemorosa (April).. ,,
Calendula officinalis (Sept.) ,,
Colchicum autumnale (Sept.) ,,
Crepis pulchra (July) .... shut.
Crocus aureus (March)......open.
Draba verna (March)........ ,,
Eranthis hiemalis (March).. ,,
Eschscholtzia Californica (June)........................ ,,
Gallasia villosa (July)...... shut.
Oxalis Acetosella (April)....open.
Tulipa sylvestris (May)...... ,,
Tussilago Farfara (April).. ,,
Veronica Chamædrys (May) ,,

10–11 A.M.
Abutilon Avicennæ (July)... open.
Anemone Pulsatilla (March) „
Anemone vernalis (March).. „
Centunculus minimus (Aug.) „
Erythræa pulchella (Aug.).. „
Lampsana communis (July) shut.
Tragopogon floccosus (July) „
Tragopogon orientalis (July) „

11–12 A.M.
Crocus lævigatus (Oct.)......open.
Hieracium amplexicaule (July) .... shut.
Mesembryanthemum crystallinum (July) ....open.
Nicandra physaloides (July) „
Sternbergia lutea (Oct.)...... „

12–1 P.M.
Sonchus arvensis (Aug.)..... shut.

1–2 P.M.
Hieracium Pilosella (July). „
Lactuca sativa (Aug.)........ „
Sonchus oleraceus (July).... „

2–3 P.M.
Cichorium Intybus (Aug.)... „
Hedypnois tubiformis (July) „
Lactuca muralis (July)...... „
Mamillaria glochidiata (Aug.)„
Solanum tuberosum (July).. „
Taraxacum officinale (June) „

3–4 P.M.
Anagallis phœnicea (July).. „
Erythræa pulchella (Aug.).. „
Eschscholtzia Californica (July) .... shut.
Gentiana utriculosa (July).. „
Helianthemum alpestre (June) „
Hieracium aurantiacum (July) .... „
Hypecoum grandiflorum (July) .... „
Lactuca Scariola (Sept.) ... „
Nicandra physaloides (July) „
Ornithogalum Narbonense (July) .... „
Oxalis Valdiviana (July)... „
Specularia Speculum (July) „

4–5 P.M.
Calendula officinalis (Sept.) „
Centunculus minimus (Aug.) „
Crocus aureus (March) ...... „
Crocus lævigatus (Oct.)...... „
Diplotaxis tenuifolia (Sept.) „
Geranium columbinum (Aug.) „
Isopyrum thalictroides (April) „
Linum grandiflorum (July) „
Linum viscosum (June)...... „
Mesembryanthemum crystallinum (July) .... „
Oxalis lasiandra (June)..... „

5–6 P.M.
Abutilon Avicennæ (July)... „
Adonis vernalis (April)...... „
Anemone Hepatica (April).. „
Anemone nemorosa (April).. „
Anemone Pulsatilla (March) „
Anemone vernalis (March).. „
Colchicum autumnale (Sept.) „
Draba verna (March) .... „
Gentiana asclepiadea (Aug.) shut.
Lactuca perennis (Aug.)..... „
Oxalis Acetosella (April) ... „
Sternbergia lutea (Oct.)...... „
Tulipa sylvestris (May)...... „
Tussilago Farfara (April).. „
Veronica Chamædrys (May) „
Veronica Persica (June)..... „

6–7 P.M.
Anoda hastata (July)........ „
Campanula Trachelium (July)„
Carlina acaulis (Aug.)...... „
Crepis rubra (July)........... „
Dianthus neglectus (July)... „
Eranthis hiemalis (March).. „
Gentiana acaulis (May)..... „
Hypochœris maculata (June) „
Silene Saxifraga (July)..... open.

7–8 P.M.
Carlina vulgaris (Aug.)..... shut.
Gentiana cruciata (July)... „
Geranium lucidum (July)... „
Gilea tricolor (July) .... „
Nymphæa alba (Aug.) ...... „
Ranunculus acer (June)..... „
Silene Vallesia (July).......open.
Tolpis barbata (Aug.)....... shut.

8–9 P.M.
Brassica oleracea (Sept.).... „
Mulgedium Plumieri (July) „
Rosa arvensis (June) .... „
Rosa rubiginosa (June)...... „
Silene nutans (June).........open.
Solanum nigrum (Sept.).... shut.

In the tables below are collated a few species whose times of opening and closing have been recorded for both Upsala and Innsbruck.

Opening of Flowers at Upsala and Innsbruck.

Name of Plant.	At Upsala.	At Innsbruck.	Difference in Hours.
Cichorium Intybus	4– 5 A.M.	6– 7 A.M.	2
Hemerocallis fulva	5 „	6– 7 „	1–2
Sonchus oleraceus	5 „	6– 7 „	1–2
Taraxacum officinale	5– 6 „	6– 7 „	1
Hypochœris maculata	6 „	7– 8 „	1–2
Sonchus arvensis	6– 7 „	7– 8 „	1
Lactuca sativa	7 „	8– 9 „	1–2
Nymphæa alba	7 „	8– 9 „	1–2
Anagallis arvensis	8 „	9–10 „	1–2
Arenaria rubra	9–10 „	10–11 „	1

CLOSING OF FLOWERS AT UPSALA AND INNSBRUCK.

NAME OF PLANT.	AT UPSALA.	AT INNSBRUCK.	DIFFERENCE IN HOURS.
Taraxacum officinale	8–10 A.M.	2–3 P.M.	5–6
Cichorium Intybus	10 „	2–3 „	4–5
Lactuca sativa	10 „	1–2 „	3–4
Sonchus arvensis	10 „	12–1 „	2–3
Sonchus oleraceus	11–12 „	1–2 „	2
Arenaria rubra	1– 3 P.M.	3–4 „	1
Hypochœris maculata	4– 5 „	6–7 „	2
Hemerocallis fulva	7– 8 „	8–9 „	1
Nymphœa alba	5 „	7–8 „	2–3

From a perusal of these tables it appears that flowers both open and close earlier in the day at Upsala than at the more southerly situated Innsbruck. This result, especially the earlier opening, is probably connected with the fact that the sun during the flowering-season of the plants in question rises about an hour and a half earlier at Upsala than at Innsbruck.

With this difference in time of opening of flowers, the results of observations carried out in mountainous districts on plants which extend from the low warm valleys up into the hills entirely harmonize. The Hepatica (*Anemone Hepatica*) blooms on the valley-floor at Innsbruck (560 metres) in March, at a time when the sun rises at 6 a.m., its flowers opening each day between 9 and 10 a.m. In the mountain glens, south of Innsbruck, at a height of 1560 metres above the sea-level, it blossoms in May, at a time when the sun rises at 5 a.m. Here its flowers open between 8 and 9 a.m. *Lampsana communis* and *Sonchus arvensis* blossom in July in the meadows of the Innthal (560 metres); in the adjacent Gschnitzthal (660 metres higher) in August. The sun rises at Innsbruck in July at 4·30, and the capitula of these two plants open in the Innthal between 6 and 7 a.m.; in August the sun rises about an hour later, and the same plants open correspondingly in the highly-situated Gschnitzthal also an hour later, *i.e.* between 7 and 8 a.m.

Several ornamental garden plants are indefatigable in their blossoming. For months on end flowers upon flowers are produced, only ceasing with the on-coming of winter. As an example *Catananche cœrulea* may be instanced; at Vienna it remains in flower from the end of June till the end of October. Its capitula show a periodic opening and closing, but they differ in the hour at which they execute their movements according to the season. At the end of June and beginning of July they open between 4 and 5 a.m., in August and in the first half of September between 5 and 6, whilst in the latter part of September and beginning of October they open between 6 and 7 a.m. Finally, in the widely-distributed Dandelion (*Taraxacum officinale*), to be met with in isolated examples flowering in spring, summer, and autumn, the same thing may be observed. In May it opens between 7 and 8, at midsummer between 6 and 7, in August between 7 and 8, and in September between 8 and 9 a.m.

The times of opening and closing given here and in the Floral Clock apply only to fine days. In cloudy, misty, and rainy weather, the flowers remain closed or only partly open; or, when these conditions are but temporary, a conspicuous retardation of opening and closing takes place, which cannot, however, be indicated numerically. Further, the observations given above relate in particular to plants well placed in regard to illumination. Such a limitation of the flowers under observation is absolutely essential, if tolerably reliable results are required. The greatest care is necessary, especially in the case of flowers which open quickly. Thus one finds with the almost suddenly-opening Gentians (*Gentiana ciliata*, *Bavarica*, and *verna*), that whilst those growing on the east or south side of a hillock have already opened wide their flowers, those a few yards away with a northerly aspect still keep their flowers closed. On luxuriant Opuntia-plants it is quite common for the flowers on the branches of the sunny side to open a long time before those on the shady side, and this with flowers of the same age.

The whole of these observations point to the fact that the opening of flowers is especially promoted by sunshine. Exactly how it is brought about, how the influence of the sun's rays in these opening-movements of flowers affects the tension of the tissues, is by no means easy of explanation. Still the question is so full of interest that it is well worth our consideration. First, we may inquire whether it is light or heat which gives the impulse to the remarkable changes in tension which lead to the movements of the petals. Plants were employed, for the solution of this question, whose flowers open directly they are reached by the first morning rays of sunshine. Specimens of *Gentiana Rhœtica* and *asclepiadea* were placed in a roomy cylinder of glass in which the temperature was maintained at a low and uniform temperature. This was effected by surrounding the cylinder by a second, larger one, and causing a stream of water of a constant temperature of 7° C. to circulate in the space between the cylinders. Since this mantle of water only permitted rays of light and not of heat to pass, it would be due solely to the action of the former if the flowers under experiment opened. As the rays of the morning sun reached the cylinder the Gentians within opened their flowers. In view of this result one is justified in assuming that the opening is occasioned by the rays of light. But that it arises solely from this cause were too hasty a conclusion, as appears from the following control-experiment, conducted upon the same Gentians. They were, whilst closed, placed in a dark room over the still hot iron of a stove in a situation where the thermometer indicated 42° C. Within 3 minutes they had all completely opened.

This apparent contradiction may be explained by the assumption that the rays of light which fell upon the closed Gentian flowers in the cylinder were converted into heat. As we know, if rays of light strike any object and are not entirely reflected from its surface, they warm it (*cf.* vol. i. p. 519). This probably is the case with the Gentians, and the phenomenon may be explained as follows. The light-vibrations are communicated to the flowers and converted into vibrations of heat. This heat produces changes in the turgidity of the tissues, affecting their tension and growth. The active energy of the heat is converted into another form of movement which ultimately alters the position of the petals, and we see the flowers opening. This explanation, further, harmonizes with the ascertained fact that under the influence of light and warmth the watery contents of certain cells in dead tissues undergo a rapid alteration, and that even in portions of flowers whose cells contain no living protoplasm changes in tension are brought about. It also agrees with the conception that the periodic opening and closing of flowers stands in relation to those chemical changes and molecular re-arrangements which we know as Respiration, Metabolism, and Growth. It has been demonstrated that flowers which exhibit periodic movements do not cease their growth on their first opening, but continue to stretch both in length and breadth. The perianth-leaves of Winter Aconites (*cf.* p. 114), Meadow Saffrons, Anemones, and Gentians, and the ligulate florets of the capitula of the Daisy, Marigold, and Leopard's Bane grow in length considerably every night. Only so long as this growth continues is an opening or closing possible, these movements cease simultaneously with growth.

The suggestion already offered as to the significance of anthocyanin (vol. i. p. 520) agrees with the idea that light is converted into heat in the tissue of the sepals. It was made probable, in the page cited, that the variously-coloured pigments known as anthocyanin possessed amongst other properties that of converting light into heat. It is particularly interesting to note that the white sepals of periodically opening and closing Anemones (*Anemone alpina, baldensis, nemorosa, sylvestris, trifolia*, &c.), show a red, violet, or blue tinge on the under side. Quite similarly coloured are the ligulate florets of many Composites (e.g. *Anacyclus officinarum, Bellis perennis, Calendula pluvialis, Hieracium Pilosella*). It is of course the under-surfaces of the sepals, petals and marginal florets of closed flowers and capitula which are alone visible. When they are closed they appear red, violet, or blue; when open, white (yellow in *Hieracium Pilosella*). The first rays of the morning sun fall first on the layers of cells coloured by anthocyanin, and we readily understand what an important part this substance may play in converting the light into heat.

Seeing that the opening of flowers and flower-buds stands to the rays of the morning sun in the relation of effect to cause, we may infer that the shutting at evening is connected with the waning light and heat. It is also to be expected that closed flowers may be made to open at will by appropriate illumination and warmth, and conversely. This at any rate holds good for a number of plants. It has been already remarked of *Gentiana nivalis* (*cf.* p. 116) that in the course of an hour, when the sun alternately shines and is obscured by clouds, it will repeatedly open and close. This is also the case with several other Gentians, with Tulips, Meadow Saffrons, and a Flax (*Linum catharticum*). In them, also, is the effect of earlier rising and later setting of the sun in northern latitudes especially conspicuous. But in the majority of flowers with periodic opening and closing, the matter is not quite so simple. True, the majority of species of Flax and Wood-sorrel, and the marginal florets of Composite heads respond to illumination and warmth by movements, as when the sun's rays reach them in the morning after the night's rest. But when, subsequently, they have once closed it is impossible to make them open again completely the same day, vary the illumination as you will. Indeed, in the majority of these flowers the closing occurs not towards sunset, but at high noon; thus the heads of *Lampsana* and *Tragopogon* shut before the sun reaches the zenith, and several hours before the maximum temperature is attained. Then, again, there are the Dame's Violet (*Hesperis matronalis*), and many Caryophyllaceæ, which only begin to open their flowers as light and temperature wane, and shut them again ere the sun has risen. To explain these movements as being a direct consequence of illumination and warmth were as futile as to explain the sleep of man and other animals as the immediate consequence of on-coming night. Undeniably there is an indirect connection with the change from light to darkness, from warmth to cold, but conceivable only in the same manner as assimilation, metabolism and growth, in plants and animals, observe the periodicity of day and night. We may state it in this way: in different organisms certain resultant effects of assimilation, metabolism and growth become manifest at different times, the particular time depending on the advantages accruing to the organism in its special circumstances. For Man the night is the most advantageous time for sleep; for Owlet Moths and other Noctuæ it is not. For *Lampsana communis* it is of advantage in respect of its ultimate self-fertilization (to be described hereafter) that its capitula should close before noon, for the Dame's Violet and numerous Catchflies (*Silene*), that their flowers should open in the evening to receive visits from Moths (*cf.* p. 154).

These observations offer no complete or satisfactory explanation. It still remains unsolved how, in so many plants, periodic movements not depending directly upon change in the environment have become hereditary. For those who are satisfied with a fine-sounding Greek or Latin word in place of an explanation, it may be remarked that these movements of floral leaves just described have been termed *Autonomous movements.*

RECEPTION OF FLOWER-SEEKING ANIMALS AT THE ENTRANCE TO THE FLOWER.

In a volume written years ago (*Plants and their Unbidden Guests*) I divided the animals which come as guests to partake of the pollen, honey, &c., of flowers into the bidden and unbidden. The former greatly profit the plant by their visits, and there exist a multiplicity of arrangements for attracting them; the latter are unprofitable and, frequently, positively disadvantageous; when they come they must be hindered and sent away. The methods of flowers for attracting bidden guests have been already described, the reception of these and the unbidden ones at the entrance to the flower must now be considered.

And first let us see what are the arrangements which exist to enable the bidden guests to obtain the food they desire without loss of time, exertion, and, most important of all, with advantage to the plant itself. It were a contradiction for the invited guests on their arrival to find the honey-secreting flower inaccessible, or that a flower should remain widely open when no more nourishment was to be obtained—when the meal, so to speak, was finished.

These obvious truisms apply to flowers still in bud, which it would be premature for insects to visit, and to such as have no further need of insects. It commonly happens that when a flower is pollinated its means of attraction—coloured or scented corolla—disarticulates and falls off. But cases exist in which the petals, having served this purpose, do not at once fall away, but are retained, having another part to play. When this is the case it is undesirable that they should interfere with the other younger flowers by competing with them for visitors; in a word, they must be rendered inaccessible. This is most frequently accomplished by the petals assuming the position they occupied in the bud, and often enough such a flower absolutely resembles a bud, as in the *Yucca,* represented in fig. 240 [1], p. 157. Sometimes a lobe of the perianth or of the sheath-like spathe folds down, obstructing the entrance, as in many Aroids, and, in particular, in the Birthwort (*Aristolochia Clematitis, cf.* fig. 257 [8]). In a number of cases the old flowers, which have no further need of insects, bend down out of the way of the younger ones, as may be seen in a number of Papilionaceæ and Boragineæ (*cf.* vol. i. p. 744). In *Morina Persica* and in the Brazilian Rubiacea, *Exostemma longiflorum,* the old flowers not only bend down, but undergo a peculiar change in colour, so that they are no longer noticed by insects. At the time of flowering the tubular corollas of these flowers are white and attractive to night-flying moths, being visible in the dark at some distance; but as soon as they are pollinated the corollas fade and bend down, assuming ere the following night a lurid red tinge, so that they are no longer visible in the dark.

It is similarly capable of easy demonstration that flowers provided with allurements for animals become conspicuous and accessible only at that period when visits are of real advantage. Their accessibility is then promoted as much as possible. In addition to being open the flowers are directed towards the side from which the visits of the most welcome guests are expected. In many plants, of which the Crown Imperial (*Fritillaria*), Foxglove (*Digitalis*), and *Campanula* may serve as types, the at first erect flower-stalks bend down sharply just before the opening of the flowers, so that the entrance is directed towards the ground. This position is inconvenient and unsuited to animals which would suck the honey, hovering over the flowers, to flies, accustomed to lick up honey from a flat surface, to such insects as are too timid to venture into the inside of a hollow flower, finally to beetles which require large amounts of deposited pollen. To bees and humble-bees, however, these flowers are accessible; supported by the projecting stigmas, style, and stamens, or sometimes by hairs, they easily climb up to the honey-secreting dome of the bell. Probably these insects prefer bell-shaped flowers, since here they have no competitors to fear. The ready welcome thus offered to the most industrious of all flower-visitants has this further advantage, that the desired transfer of pollen from plant to plant is accomplished with certainty and despatch; it may be said of these hanging bell-flowers that they are directed towards the side from which the most welcome of all guests will reach them. Nor must it be forgotten that from this pendent position accrue many other advantages; thus the pollen is well protected from wet by the corolla (*cf.* p. 118), and numerous little Hymenoptera, useful in carrying pollen, use these bells as night-quarters (*cf.* p. 163).

In a large number of plants, though the closed buds are directed upwards, the flower-stalks bend down on opening, so that the entrance to the flower is directed sideways. When, at length, insect-visits are no further required, the older flowers collapse and point downwards. This change in the direction of the flower may be well observed in Honeysuckle (*Lonicera*), Evening Primrose (*Œnothera*), *Acanthus*, in Balsams (*Impatiens*), *Galega*, *Melilotus*, and many of the Clovers (*Trifolium*, *cf.* fig. 252 [9] p. 184).

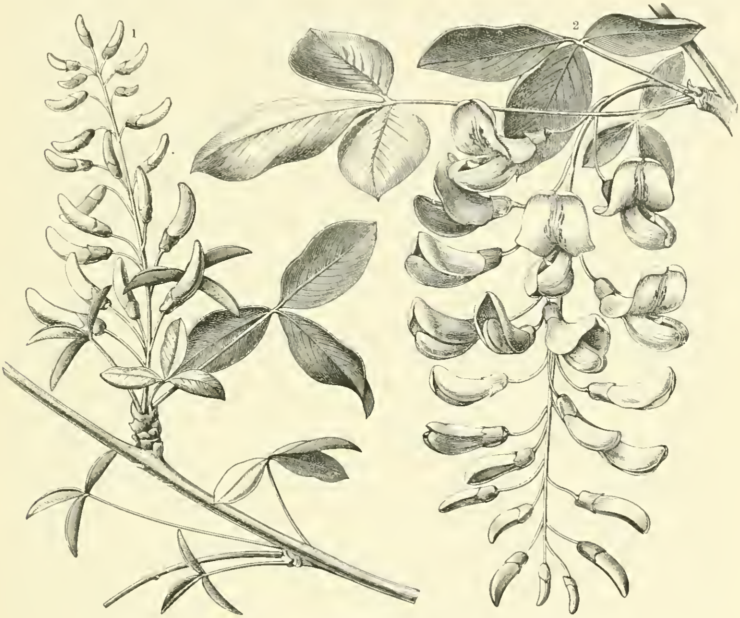


Fig. 256.—Preparation of Flowers for Insect-visits in the Laburnum (*Cytisus Laburnum*).

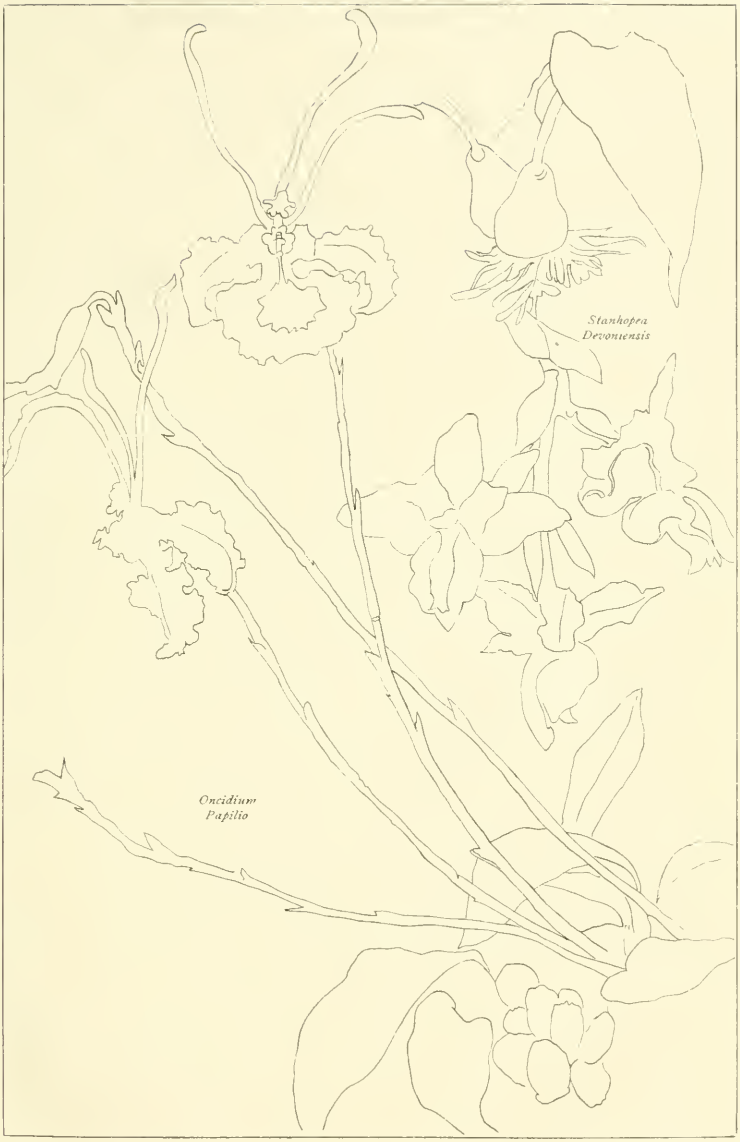
[1] Erect raceme; all the flowers still closed. [2] Pendent raceme; some of the flowers open.

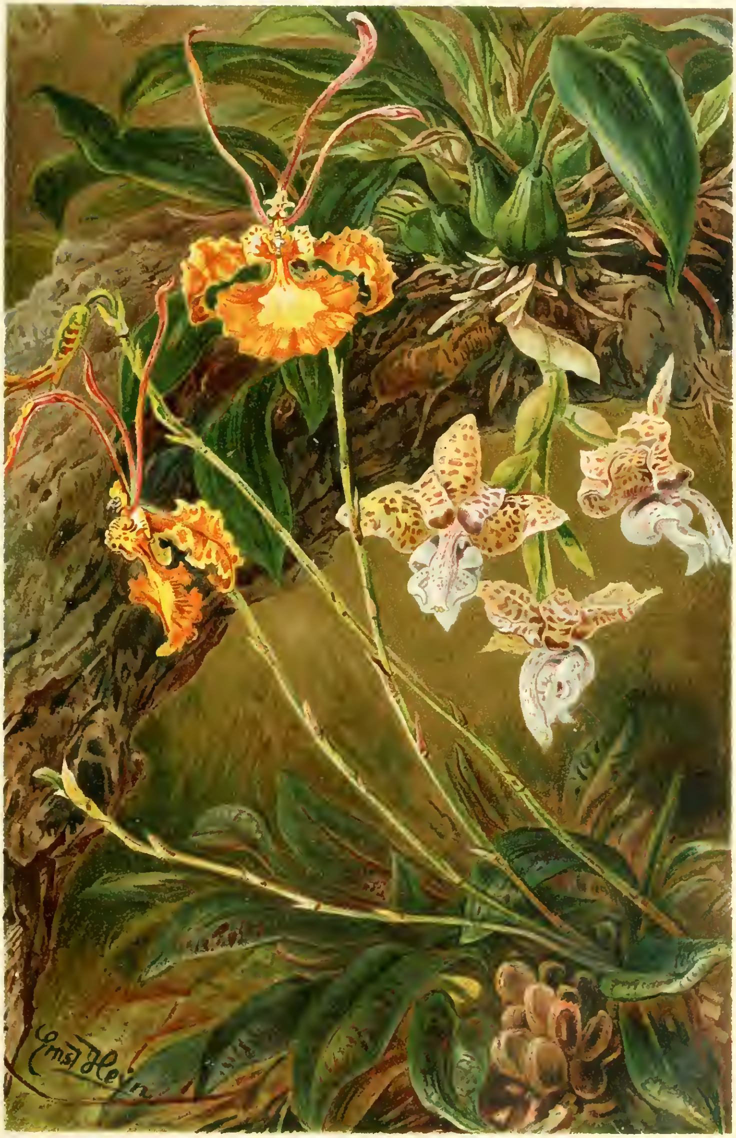
Very peculiar is the behaviour in a number of Papilionaceæ, of which the Laburnum (*Cytisus Laburnum*) may be taken as type (*cf.* fig. 256). The axis of the raceme remains erect so long as all the flowers of the inflorescence are in bud, the individual flowers being so placed that the standard is above and the keel below (fig. 256[1]); later, the rachis becomes pendent, and the apex of the inflorescence points downwards. The buds are now so placed that the standard is below. Before the standard unfurls and the flowers become accessible, however, the stalk of each flower twists round through nearly 180°, so that the standard is again brought uppermost (*cf.* fig. 256[2]). In this position the keel is a convenient platform for visiting insects to alight upon. It is of interest to note that if the young racemes are forcibly retained in the erect position by means of strings, the twisting of the flower-stalks does not occur, or only to a very slight extent. In the nearly allied *Laburnum Alschingeri* the racemes are always borne erect, and there is no twisting of the stalks at all; by this character the two species may be readily distinguished.

Many examples of the same phenomenon are furnished by Orchids. Here, however, the twisting is accomplished not by true flower-stalks but by the stalk-like inferior ovaries. In Orchid flowers one member of the perianth, the lip or labellum, is conspicuous by its shape and size, and serves in more than two-thirds of all Orchids as a landing-stage for insects. This petal is directed upwards in the bud, and in a few Orchids always retains this position, as in the vanilla-scented *Nigritella* and in *Epipogium* (*cf.* fig. 257[10]). But in the majority of Orchids, such, for example, as grow in the meadows with erect spikes of flowers, the ovary undergoes a spiral twisting which brings the lip below so as to serve as a platform for the insects. Nor is this confined to our indigenous Orchids; it occurs also in tropical, epiphytic forms which grow perched on branches of trees or ledges of rock, when they have an upright rachis to the inflorescence; as, for instance, in *Oncidium Papilio,* represented in the accompanying Plate XIII., entitled, "West Indian Orchids". Many of these epiphytic Orchids, however, have not ascending but more or less pendent inflorescences; this is markedly the case in *Stanhopea,* of which a species, *Stanhopca Devoniensis,* is represented in the plate beside the *Oncidium.* Such flowers do not require to twist to bring the lip into the position in question. Indeed, in this and many other similar Orchids no twisting of the ovary takes place. If, however, a young spike of *Stanhopea* be fixed in an erect position, the flowers will all twist within twenty-four hours and take up the position which they would have occupied had the inflorescence been pendulous.

Altogether peculiar is the state of affairs in *Gongora galatea,* a tropical American Orchid sometimes introduced into European hot-houses. As in *Stanhopea,* the spikes are pendulous from the branches of old trees, but the lip of the flower in its original position below is unsuited as a platform for insects. Consequently the ovaries twist through 180°, so that the lip stands above and is of service to visiting insects.

It is an interesting circumstance that all the flowers on many erect, flowering axes turn towards the same side, so that a one-sided spike or raceme results, as in *Vicia, Digitalis, Corydalis,* and *Penstemon.* The entrance to the flowers is directed towards the side from which the visits of insects or humming-birds may be expected. When, for instance, a Foxglove (*Digitalis*) grows by the edge of a wood,


Stanhopea Devoniensis
Oncidium Papilio



WEST INDIAN ORCHIDS.

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it turns all its flowers away from the shaded side where insects are not abundant, and directs them towards the sunny meadow swarming with bees and humble-bees. Some Labiates belonging to the genera *Salvia* and *Satureja* turn all their flowers one way only when they stand close to a steep wall. When they are equally exposed on all sides their flowers are directed towards all the points of the compass. A similar behaviour is observable in many plants which grow on the narrow mouldings of old, ruined walls, or on the ledges of steep rock faces, as, for instance, in the Snapdragon (*Antirrhinum majus*) and in *Haberlea rhodopensis* of the Balkans; both of these turn their flowers away from the wall or rock, even when these backgrounds are well warmed and lighted by the sun.

The visitors to laterally-directed flowers include Syrphidæ, Owlet-moths, Hawk-moths, Humming-birds—indeed all animals which suck honey whilst hovering in front of the flowers. As they require no platform, we find all flowers of this type destitute of anything of the kind.

Flowers which are visited by sun-birds (Nectariniæ), humming-birds and by night-flying moths are likewise destitute of plates, ridges, fringes, pegs, or knobs on which the animals might alight or cling. The lobes of the corolla which close the flower in bud take, on opening, a position in which they are useless as perches; indeed they bend right back so as to impede the hovering animals as little as possible as they suck up the honey with their probosces or bills. As examples may be mentioned the Honeysuckle (*Lonicera Caprifolium*), the Orchid *Habenaria bifolia* visited by Hawk-moths, and *Melianthus major* sought by small honey-drinking sun-birds (*cf.* figs. 258 [9, 10, 11, 12, 13]). When a well-developed edging or fringe is present in flowers adapted to crepuscular Lepidoptera and Humming-birds, as in *Mirabilis longiflora, Nicotiana affinis, Posoqueria fragrans, Narcissus poeticus,* and *Œnothera biennis,* it serves from its delicacy and position not as a platform, but, in virtue of its conspicuous white or yellow colour, as an attractive organ visible at a considerable distance in the gloaming.

Otherwise is it with flying animals which must first alight on the flower and then penetrate to the concealed honey. Like doves entering a dove-cote, they require a platform, and in point of fact such a provision is found in such laterally-directed flowers as depend on this class of visitor.

In *Epipogium aphyllum* the "column" pointing obliquely downwards forms a convenient platform for humble-bees (*Bombus lucorum, cf.* figs. 257 [10, 12, 13]). But on the whole the column of Orchid-flowers is rarely used in this way. Very often the stamens or style project well beyond the margin of the flower and serve this purpose, as, for instance, in the Horse Chestnut (*Æsculus*), many Liliaceæ (*Funkia, Anthericum, Paradisia, Phalangium*), Viper's Bugloss (*Echium*), *Dictamnus* and *Pæderota,* similarly in the large-flowered Speedwells (*Veronica, cf.* fig. 257 [1]). More frequently, however, the margin of the perianth or corolla is modified for this purpose. Especially noteworthy in this respect are the Aristolochias, on the flowers of which there exists an almost endless series of sometimes flattened, sometimes perch-like, alighting-platforms. In *Aristolochia ringens* (fig. 242, p. 166), it resembles a sugar-scoop; in the Brazilian *Aristolochia labiosa* (fig. 257^{6}), there is a broad heart-shaped expansion in front of the narrow entrance to the flower; in *Aristolochia cordata* (fig. 257^{7}) there is an elongated, flagelliform perch for the flies; whilst in our own *Aristolochia Clematitis* (figs. 257^{8} and 257^{9}) there is a slightly excavated lip on which the midges can alight before entering the flower.

A multifarious variety of arrangements is met with in the perianths of Orchids and in the corollas of bi-labiate flowers for promoting access to the flowers. There are all sorts of lobings and sinuses, fringes, pegs, and knobs on the lower lip which serve as landing-stages for alighting and as fulcrums for further explorations to numerous flies, wasps, bees, humble-bees, and butterflies. In the noble Orchid *Phalænopsis Schilleriana* (*cf.* fig. 258^{1}) the smooth and complex labellum has a little projection not far from its point of attachment which resembles, and indeed serves, as a footstool to the visiting flies. Behind the footstool is the column, the apex of which is occupied by the anther, and whose lower portion is excavated into

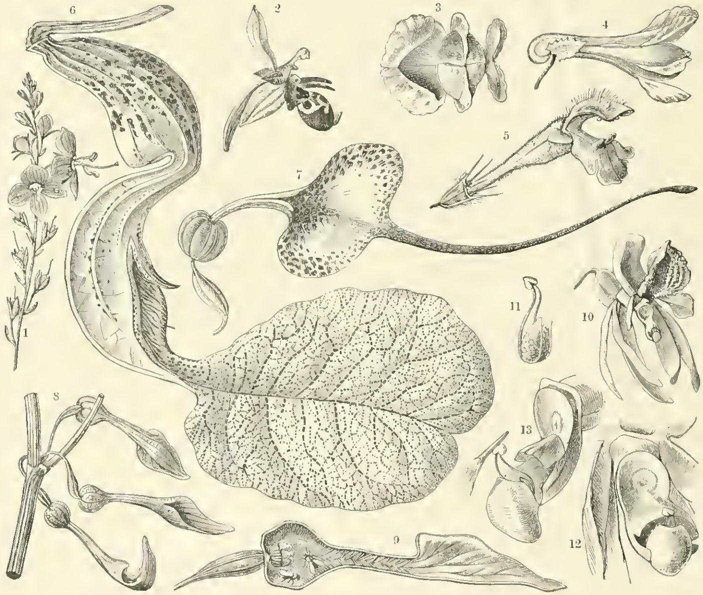


Fig. 257.—Arrangements for the reception of Insects at the entrance to the Flower.

^{1} *Veronica Chamædrys.* ^{2} *Ophrys cornuta.* ^{3} *Corydalis lutea,* from the front. ^{4} The same, from the side. ^{5} *Galeopsis grandiflora.* ^{6} *Aristolochia labiosa.* ^{7} *Aristolochia cordata.* ^{8} *Aristolochia Clematitis*; the lowermost flower is faded and has bent down, its lip is folded over the entrance to the flower. ^{9} Longitudinal section of a flower of *Aristolochia Clematitis*; within the enlarged cavity of the flower are two midges (*Ceratopogon*) temporarily imprisoned by the reversed hairs of the tube. ^{10} Flower of *Epipogium aphyllum.* ^{11} Pollinia of *Epipogium.* ^{12} Column of *Epipogium* showing the small heart-shaped rostellum. ^{13} Shows the pollinia of *Epipogium* attached by their sticky rostellum to a pencil, in process of withdrawal. $^{9, 11, 12, 13}$ somewhat enlarged; the other figures natural size.

a stigmatic cavity. Leading into the honey-lined stigmatic cavity is a circular aperture or window, and projecting into the upper margin of this window is the little pointed, triangular rostellum like the bill of a bird (fig. 258^{2}). When a fly desires to abstract honey from the stigmatic cavity, it stands on the footstool and puts its head in at the window (fig. 258^{5}). In doing so it touches the extremely sticky tip of the rostellum, which sticks to the top of its head. When satisfied, the fly, in vacating the footstool, drags the two pollinia (pollen-masses), which are attached to the rostellum, out of the anther, and goes away with them on its head (258^{6}). It now visits another flower and again alights upon the footstool. Meanwhile the stalk of the two pollinia has bent forwards, like a swan's neck (258^{7}), and as the fly puts its head in at the window the pollinia precede it into the stigmatic cavity and remain sticking to the wall (258^{8}).

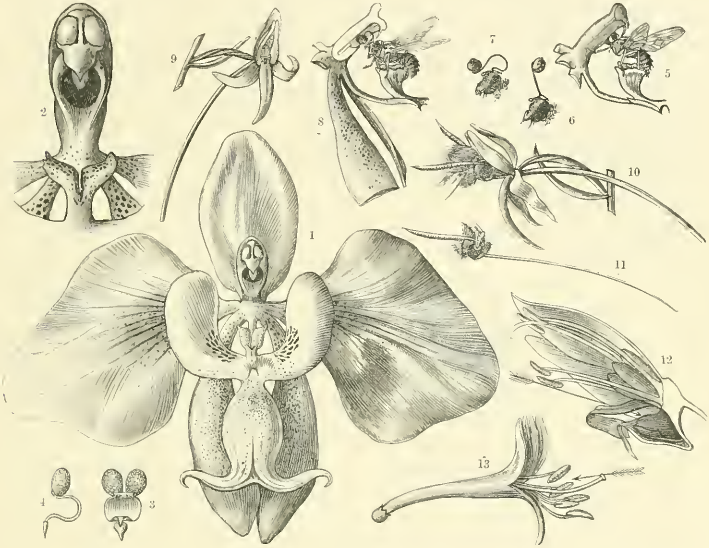


Fig. 258.—Arrangements for the reception of Insects at the entrance to the Flower.

^{1} Flower of *Phalænopsis Schilleriana.* ^{2} Column of this *Phalænopsis*; in front of it is the little bi-lobed footstool. ^{3} Pollinia of *Phalænopsis* with heart-shaped gland; seen from in front. ^{4} The same, seen from the side. ^{5} A Fly which has alighted upon the footstool is introducing its head into the stigmatic cavity, and simultaneously becoming attached to the gland. ^{6} Head of the Fly with attached pollinia. ^{7} The same, the stalk of the pollinia has become bent like a swan's neck. ^{8} A Fly introducing the pollinia into the stigmatic cavity of another flower; the column is shown in longitudinal section. ^{9} Flower of *Habenaria bifolia.* ^{10} The same flower visited by *Sphinx pinastri*; the head of the Sphinx alone is represented, its proboscis has been introduced into the long spur. ^{11} Head of *Sphinx pinastri* with long proboscis. ^{12} Flower of *Melianthus major*, seen from the side, after removal of some of the petals. ^{13} Flower of *Lonicera Etrusca.* ^{2}, ^{3}, ^{4}, ^{6}, ^{7} slightly enlarged; the other figures natural size.

Remarkable, also, is the threshold provided for alighting insects on the lower lip of *Ophrys cornuta* and of the Hemp-nettle (*Galeopsis Tetrahit*). The lip of the former has two hollow projecting pegs which give the whole flower a horned appearance (fig. 257 [2]), that of the latter two pegs, also hollow (fig. 257 [5]). In the Snapdragon (*Antirrhinum*) and in the allied Toad-flax (*Linaria*) two remarkable knobs, projecting from the lower lip, serve as a platform for insects which, by exerting pressure, force down the lower lip and gain access to the flower. It is most entertaining to observe how a Humble-bee buzzes about till it alights on the two knobs of the lower lip, and then, having opened the mouth by means of hinges on either side of the corolla, suddenly disappears into the cavity of the flower to fetch honey. In the Calceolarias the phenomenon is even more remarkable. The Humble-bee sits on the inflated, slipper-like lower lip, and opens the mouth by a light pressure against the upper lip. Then a nectary, hitherto hidden in the slipper-like cavity, comes to light, flap-like, and amply provided with honey. This nectary is presented to the Humble-bee just like a spoon as it sits on the lower lip. Directly the bee goes the lower lip snaps to, and the nectary disappears from view.

An interesting mechanism obtains in the flower of *Corydalis lutea* (*cf.* figs. 257 [3] and 257 [4]). The corolla here consists of four petals, one right and one left, one above and one below. The two latter are similar and applied together like two hollow hands. The right-hand petal is small and spoon-shaped, the left-hand one is the largest of all, and is produced outwards into a short spur which contains honey, whilst above it expands into a sort of brim. Access to the honey is obtained beneath this brim, and insects must enter here. To accomplish this the insect sits on the two median petals, which are applied together (fig. 257 [3]). But to give it a better hold, each of these petals has a median flap, which may be compared to stirrups on either side of a saddle. On these the bee gets a purchase, sitting as it were on a saddle. It may be noted here incidentally that the pollen is scattered on the under surface of the abdomen of the insect by a curious lever-mechanism; also that *Corydalis* is almost unique amongst flowers in that it is lob-sided, *i.e.* the spurred petal is not in the median plane of the flower (as in the generality of zygomorphic flowers) but is inserted laterally.

Many Papilionaceous flowers have a considerable resemblance to *Corydalis*, although their flowers are constructed on quite a different plan. The Papilionaceous flower has five petals. Of these the two front ones are united together and form the "keel", the two lateral are known as the "wings", whilst the posterior unpaired one is expanded and is known as the "standard". This standard closes the entrance to the base of the flower, where the honey is concealed, from behind so that insects seeking honey must sit either on the keel or wings. In the flowers of Sainfoin (*Onobrychis*) the wings are quite small and invisible, and here the relatively big keel serves as alighting-platform. In many others, on the other hand, *e.g.* in *Coronia*, *Orobus*, *Lotus*, and *Spartium*, the wings are folded over the keel, and meeting in the middle form a sort of cushion well suited as the alighting-place of insects.

All the flowers so far described have the peculiarity that their petals are not symmetrically arranged all round. Their right and left halves agree absolutely, but the upper and under halves are quite different. In this respect they are comparable to the face of a man, to the head of a vertebrate, or to the body of an insect—indeed many of these flowers resemble the heads of animals or flies, butterflies, spiders, &c. (cf. *Oncidium Papilio* and *Stanhopea Devoniensis*, Plate XIII. p. 224, and *Ophrys cornuta* and *Galeopsis grandiflora*, figs. 257 [2] and 257 [5]). Flowers exhibiting this kind of bi-lateral symmetry are known as *Zygomorphic*. Undoubtedly this Zygomorphy of laterally-directed flowers is connected with the formation of a landing-stage suitable for particular insects to alight upon. The Zygomorphy of *Corydalis* is peculiar, as noted at the end of the last paragraph but one.

In flowers whose opening is directed upwards, quite apart from its nature, whether it be the mouth of a narrow tube or the broad edge of an expanded plate, Zygomorphy is superfluous. Such flowers are constructed symmetrically on every side. Their petals are placed like the spokes of a wheel or the rays of a star; they have been termed *Actinomorphic*.

Such flowers, directed upwards, present a landing-stage to insects either at the periphery or at the centre. Humble-bees which visit the erect, open flowers of Gentians (*Gentiana asclepiadea, pannonicæ, Pneumonanthe, punctata*) alight first on the edge of the corolla, and then climb down into the wide tube, disappearing whilst they suck the honey. In the majority of cases, however, the edge of the corolla is so extremely delicate and flimsy that heavy insects, such as beetles, would not be adequately supported, but would bend the corolla right down on to the middle of the flower. Thus, in such flowers we frequently find an expanded disc-like or star-shaped stigma which forms an admirable platform, as in the flowers of *Tulipa*, *Paris*, *Opuntia*, *Papaver*, and *Argemone* (*cf.* fig. 243, p. 168). In Roses, Buttercups, and Anemones a large number of carpels

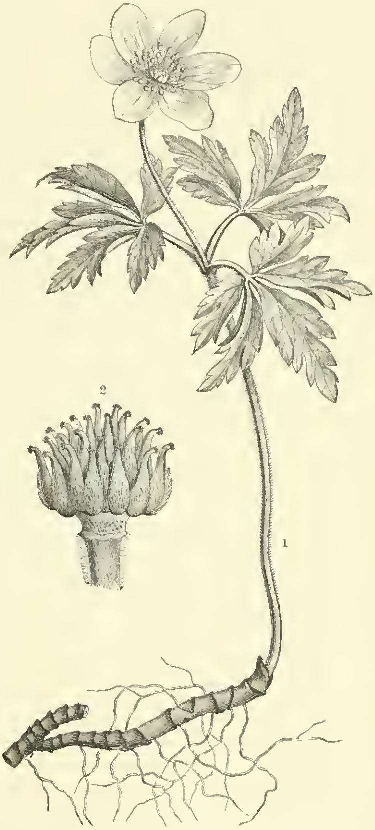


Fig. 259.—Wood Anemone (*Anemone nemorosa*).

1 Complete plant, natural size. 2 The collection of carpels from the centre of the flower; magnified.

are present in the centre forming a sort of fascicle which makes a useful platform (*cf.* fig. 259). Or, again, the style or stigma may be lobed or forked, the branches taking an oblique or horizontal position, thus resembling a perch (e.g. *Convolvulus arvensis* and *Siculus*). Or, it may be formed by the fascicled stamens in many upright, actinomorphic flowers, as in Myrtles, St. John's-Worts, the Australian Acacias and various Malvaceæ (at least in the first stage of flowering).

The Pinks and Scabiouses whose capitate flowers contain honey deep down are preferably visited by Lepidoptera, the flowers of Umbelliferæ and Euphorbiaceæ, whose honey is exposed and easy of access, by Flies, Wasps and other short-lipped Hymenoptera. To the inflorescences of Composites and Proteaceæ, the most various insects are attracted, according to the form and position of the whole inflorescence and the depth at which honey and pollen are to be obtained. It is impossible to enumerate the various cases here for lack of space, nor, indeed, would it be desirable. One more plant, *Dryandra*, one of the Proteaceæ, deserves a brief description, however, on account of the remarkable form of its inflorescence. This plant is a low shrub, a constituent of the Australian "Scrub". Its flowers are arranged around the margin of a cup about 4 centimetres in diameter. The bottom of the cup is lined with scales only, and here collect drops of liquid secreted by the flowers, which smell like sour milk. Around the margin of the cup the long styles project like pins, bent slightly inwards. The pollen is collected at the tops of the styles at the commencement of flowering; subsequently the stigmas are developed, ready to receive pollen brought by animals from other flowers. So far as is known, this arrangement of flowers and sap is not adapted to insects. It seems probable that Kangaroos visit these flowers, stick their snouts into the excavated inflorescences to drink up the sap, and unconsciously dust their mouths round with pollen which is subsequently conveyed to the stigmas. The respective heights of the *Dryandra* bushes and of Kangaroos, and the configuration of the inflorescence compared with the snout of this animal, render the assumption a not impossible one.

The efficacy of all these arrangements for promoting the quick and easy obtaining of food from flowers by "bidden guests" is obviously much enhanced by the existence of others for the exclusion of hurtful and undesired visitants. As hurtful may be characterized all such animals whose visits interfere with or prevent the speedy transfer of pollen from flower to flower. Such are small wingless animals which must of necessity reach the honey and pollen on foot. Let us consider the case of one of these little pedestrians. Suppose it to have reached a flower and covered itself with pollen; it has now before it, in order to transfer this pollen to a stigma on another plant, a long and toilsome journey beset with dangers for the pollen, quite apart from the length of time taken. The pollen may be so easily rubbed off on the journey by hairs and other structures encountered, or it may be washed off by rain. Then, even if a second flower be attained, what are the probabilities of its being in a receptive condition? How otherwise it is with the lightly-flying insects and humming-birds! They dart from plant to plant with extraordinary rapidity and visit half-a-dozen flowers within a minute or so, thus transferring the pollen new and fresh. Winged insects and humming-birds are ideal agents for the crossing of flowers, and are the most welcomed of all guests. But even of these fleet emissaries all are not equally welcome. Of what service is it to a plant if its pollen is not deposited on the proper spot—on the stigma where it can develop pollen-tubes—be the transfer accomplished ever so quickly? Let us suppose a tiny fly entering the flower of a Foxglove. It alights on the lower lip of the corolla and makes its way to the honey at the base of the flower where the honey is, without touching the stigma or stamens placed just below the upper lip. Having satisfied itself, it retreats by the same route. What advantage does the flower get from the visit of this particular insect? None. And more than this, it has been robbed of a portion of that honey on which it relied to allure some larger animal which would unintentionally stroke the anthers and stigma with its body. By the admission of small flies to Foxglove flowers consequently no transfer of pollen would be effected. Thus we see that not all flying animals are desirable visitants; that many insects, which, in consequence of their size and shape are unable to promote a transfer of pollen, must be regarded as unbidden guests, and prevented access to the honey.

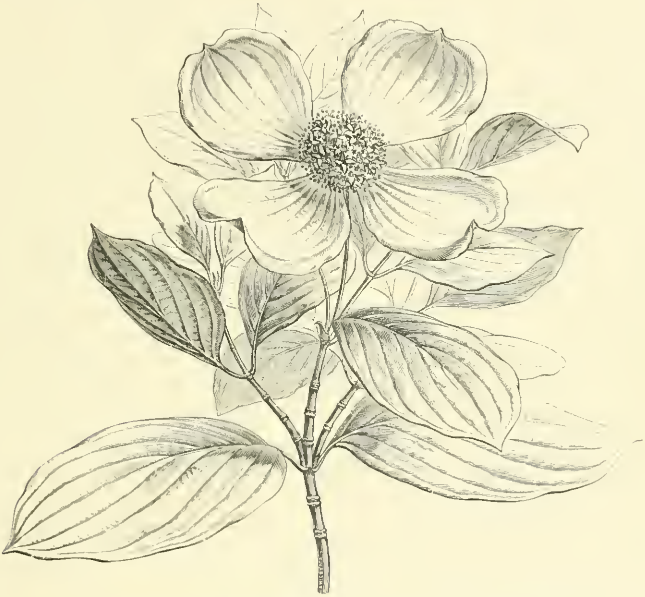


Fig. 260.—*Cornus florida*; numerous small, aggregated flowers surrounded by four huge bracts, which serve at once as attractive-organs and alighting-platforms for insects. (After Baillon.)

Nor are arrangements such as are indicated above wanting. Peculiar folds and cushions, walls and gratings, brushes and thickets of hairs are present, guarding the entrance and rendering access difficult, whilst still allowing it. Large and powerful animals find these obstacles no hindrance, and readily brush them aside; small ones, however, cannot do this, but have to climb over or circumvent the obstacles. And in many cases this enforced divergence by small insects from the direct path brings about the desired result. For, in circumventing these folds and barricades and hairs, they are unconsciously led past the anthers and stigmas, contact with which is unavoidable. Thus, what would otherwise be useless visitants become welcome guests. They are conducted indirectly to the honey by these curious structures, which may, in a sense, be termed "path-finders".

A more detailed consideration of these arrangements will be given when treating of the taking up of pollen by insects, in the next chapter. Mention of them cannot be omitted here owing to the difficulty of drawing an absolute distinction between contrivances designed to lead insects by a particular route into the flower, and such as entirely exclude the unbidden guests. The same difficulty obtains between the defences erected against wingless and those against winged insects, it being in many cases not easy to distinguish between them. Consequently, the grouping of these mechanisms in the sequel cannot be entirely free from the reproach of partiality; still it will serve its purpose should it render these problems more intelligible.

First of all, we will describe the mechanisms which serve to protect flowers against little wingless marauders which creep up from the ground. Remarkable amongst these is the indirect protection afforded to the floral honey by honey secreted in the region of the foliage. This may be seen in many Balsams, especially well in the Himalayan *Impatiens tricornis*. In this plant the stipules, which stand right and left at the bases of the leaves, are modified into secretory glands. Of the two glands, one is small and rudimentary, but the other extremely well-developed. The latter is a fleshy convex disc fused partly with the base of the leaf and partly with the surface of the stem, and so disposed that insects creeping up the stem must encounter it. The honey, secreted by the tissue of this gland, collects in a drop on the hemispherical and downwardly-directed cushion of this disc. Thus are the insects tempted by the way in their ascent. They find drops of honey provided for them at the base of every foliage-leaf equalling that of the flowers in quality and surpassing it in quantity; besides which it is nearer and more accessible. The honey-loving ants lick it up eagerly, and are content not to stray further upwards. Actual observation shows that the flowers of *Impatiens tricornis* are free from ants, whilst these stipular nectaries are much frequented by them. Their presence in the flowers is very undesirable, since they could readily get at the honey there without touching the pollen or stigma. And more than this; they would not only pilfer the honey, but they would also drive away those winged insects for which the honey is prepared—the welcome guests that pollinate the flowers. We are justified on the facts in regarding this diversion of the unbidden guests as an indirect protection of the floral honey.

This secretion of honey from the stipules in *Impatiens tricornis* begins just at the time when the plant commences flowering. This must be emphasized because the suggestion has been made that the stipular secretion serves to protect the foliage indirectly from the ravages of caterpillars, snails, and beetles. The remarkable observation has been made upon several plants, for the most part tropical, that they live symbiotically with certain small and very fierce ants. The plants afford the ants lodging in special cavities and give them nourishment in the form of sugary and albuminous secretions: the ants in return defend the foliage against the attacks of leaf-eating animals. So soon as this "standing army" of ants detects the foe it commences offensive operations, like the garrison of a fortress, and by biting and squirting formic acid frightens the invader away. In this way is protected the foliage of *Acacia spadicigera* and *sphærocephala, Cecropia peltata, Clerodendron fistulosum, Rosa Banksiæ,* and several other plants (known as *Myrmecophilous Plants*) against the attacks of leaf-eating animals. At the conclusion of this chapter opportunity will offer to describe how the flower-buds of several Composites are similarly protected against herbivorous beetles. In the case of *Impatiens tricornis,* however, the ants are no protection for the foliage; whilst the leaves are developing, no honey is secreted and no ants are present, and later, when honey is present in plenty, and the ants are licking it up, they pay no attention, even though the adjacent leaf-blades be touched or injured.

Next to the diversion of creeping animals by means of nectaries scattered over the stem and foliage may be ranked several arrangements in which the protection afforded is of a similar indirect character. Some of these have a remarkable resemblance to the devices often employed by gardeners to shield the plants in their propagating-pits and nurseries from the ravages of snails, caterpillars, centipedes, earwigs, and other noxious insects. In order to preserve a hot-house-plant from the visits of these undesirable members of the Animal Kingdom, gardeners very frequently place the pot containing the plant in question upon another low pot inverted in a shallow dish of water; thus the plant stands, as it were, on an island, and is inaccessible to the various creeping animals indicated. Similarly in a nursery the crowns of the young trees are protected against creeping vermin by tying a sticky cloth round the stem or painting the bark with bird-lime or other sticky substance. Insects attempting to climb a tree under these circumstances become imprisoned in the girdle. Caterpillars, snails, and other animals with soft integument are often excluded by attaching belts of prickly branches to the stems.

When these expedients of the gardener are compared with many of the arrangements met with in nature for the protection especially of the honey and pollen, a remarkable similarity is at once obvious. Isolation by water, prevention of access by means of sticky secretions, rings and fringes of prickles and thorns directed so as to oppose visitors on foot—such, for the most part, are the methods employed by plants to secure immunity from would-be pilferers of their honey and pollen.

Isolation by water obtains in the case of innumerable aquatic and bog-plants. The flowers of Water-Lilies, of which the *Victoria regia*, represented in Plate XI., may serve as type, the flowers and inflorescences of the Flowering Rush (*Butomus*), of the Arrowhead (*Sagittaria*), of the Water Plantain (*Alisma*), of the Feather-foil (*Hottonia*), of Bladderwort (*Utricularia*), Villarsia (*Limnanthemum*), Frog-bit (*Hydrocharis*), Water Soldier (*Stratiotes*), and of many other plants are amply protected by the belt of water which their situation involves. Flies and beetles which come through the air for honey and pollen are welcome visitors, promoting, as they do, a crossing of the pollen; snails, centipedes, &c. are, on the other hand, kept back by the water. The basins of water formed by the bases of the leaves in the Teasel (*Dipsacus*) and *Silphium perfoliatum* (figured, vol. i. p. 239), serve a like purpose, as also do the collections of water in the funnel-like sheaths of the leaves of many Bromeliaceæ (*Æchmea, Billbergia, Lamprococcus, Tillandsia*, &c.), though this is supplemented by other advantages derived by these plants from the receptacles of water in question (*cf.* vol. i. p. 241).

More frequently even than by water the flowers obtain immunity from these visitors by *sticky secretions.* The substance formed in many cases resembles bird-lime in properties, though its chemical constitution is not fully ascertained; in others it is allied to gum-arabic, or cherry-gum; whilst in others again it is a resin or a mixture of resin and mucilage known by the name of gum-resin. Occasionally this purpose is served by latex, which readily escapes from the brittle tissues and coagulates on the surface into an adhesive substance. This last method obtains particularly in certain Asclepiads, and in many species of Lettuce (e.g. *Lactuca angustana, sativa, Scariola*). The involucral scales which inclose the flower-heads of these plants are smooth and tense, and abound in latex. No obstacle prevents creeping insects, especially ants, from climbing up to this point; but as soon as the ants reach these scales on their way to the flowers, and touch the turgid investing cell-layers, they rupture the walls of the latex-tubes (which in some cases actually project as tiny hairs on the surface) with the claws of their feet, and the milk runs out in little droplets. Their feet and abdomens are smeared with latex, and when the ant bites at the substance of the scales in self-defence its head also becomes involved in the sticky mess. It seeks to free itself of this encumbrance in a variety of ways, but the result of all these struggles is merely a further rupturing of the epidermis and discharge of latex, which adds to the embarrassment of the ant. Some of these creatures manage to escape and drop to the ground, others, not so fortunate, are glued in the coagulating latex, where their dead bodies may be seen decorating the involucre of the capitulum.

The other adhesive substances mentioned arise either from certain circumscribed cells of the flat epidermis of the stem, or else definite projecting structures known as glands, glandular hairs, capitate hairs, &c., are specialized for this purpose. In the case of flat epidermal cells, the secretion is passed out from the cells and collects between the inner and outer layers of the external wall, in other words, under the cuticle. The cuticle is gradually raised up like a blister till it bursts and the sticky matter escapes. Such portions of the stem or flower-stalk resemble limed twigs, and might have been painted with the viscid substance. In the case of definite glands, the secretion, for the most part, diffuses through the walls to the surface, though in some cases the blister-method may obtain here also. Sometimes the secretion is freed by actual rupture of the delicate walls of the glandular cells.

Sticky secretions as protection for flowers against creeping animals occur most frequently on the flower-stalks, or on the main axis of the inflorescence. The popular names of several plants indicate at once their sticky character, as, for instance, the Catchfly (*Silene*), and the Viscid Lychnis (*Lychnis Viscaria*). So also, with their botanical names indicative of their adhesive character and of the insects caught by them, e.g. *Silene muscipula*, *Roridula muscipula*, and the specifications *viscidus*, *viscosus*, *viscosissimus*, *glutinosus*, and the like—names frequently occurring amongst the Scrophulariaceæ, Labiatæ, Caryophyllaceæ, and in the genera *Ledum*, *Cistus*, *Linum*, *Aquilegia*, and *Robinia*. That the protection afforded by these limed stems is essentially *floral* is particularly well shown in the Caryophyllaceous genera *Dianthus*, *Lychnis*, and *Silene*. The lower portion of the stem in these plants (e.g. *Dianthus viscidus*, *Lychnis Viscaria*, *Silene muscipula*) is green, and shows no trace of the sticky brown coating which is first met with below the pair of leaves subtending the flowering axes. And here it is only the upper portion of the internode, the portion in the immediate neighbourhood of the flowers that is sticky (*cf.* fig. 238, p. 154).

More frequent than a simple sticky coat is the presence of glands and glandular hairs on the flower-stalk, or on the outside of the flower itself, to which little animals climbing up the plant become adherent. Of this condition numerous examples are represented in fig. 261.

A rarely-occurring condition obtains in the flowers of *Cuphea micropetala* (fig. 262). The petals in this plant are reduced to tiny scales inserted at the top of niche-like excavations of the calyx (fig. 262 ^{4}). The calyx is tubular and coloured, 22–28 mm. in length, and 6–7 mm. in diameter; at the base behind the ovary it is expanded into a honey-receptacle. The ovary is relatively large and obliquely placed, forming a sort of "elbow" at the point of articulation of the style which touches the upper wall of the calyx-tube (262 ^{2}). Since the side-walls of the calyx are in close contact with the ovary, the honey-receptacle is cut off from the general cavity of the flower, as it were, by a plug. Right and left in the ovary, however, are two grooves, slightly wider in front; these form (with the calyx) two tiny canals, about half a millimetre in diameter, by which access may be had to the honey-cavity behind the ovary; usually these canals are more or less filled with honey (*cf.* figs. 262 ^{2} and 262 ^{3}, the latter showing the orifices of the two canals and elucidating the relations of the parts). To obtain the honey, flying insects must introduce their probosces into one of these canals. The admission of little ants to these flowers, insects useless for purposes of pollination, and likely to block up the honey-orifices for authorized visitors, would be disadvantageous. The arrangements which prevail for the exclusion of ants are so elaborate that one would think that the honey of *Cuphea micropetala* was for them quite irresistible. The mouth of the flower is rendered quite inaccessible to ants and other minute creeping insects by a fringe of tufts, each bearing a number of divergent sticky bristles (262$^{1, 2, 4}$). These bristles form in the aggregate a *chevaux-de-frise*, guarding the mouth of the calyx-tube, through which these small visitors cannot penetrate. Flying insects, however, which can reach the honey hovering at the mouth of the flower, and such as can use the projecting stamens or stigma as support are not impeded by the bristles, and are, so to speak, welcomed by the flowers of *Cuphea micropetala*.

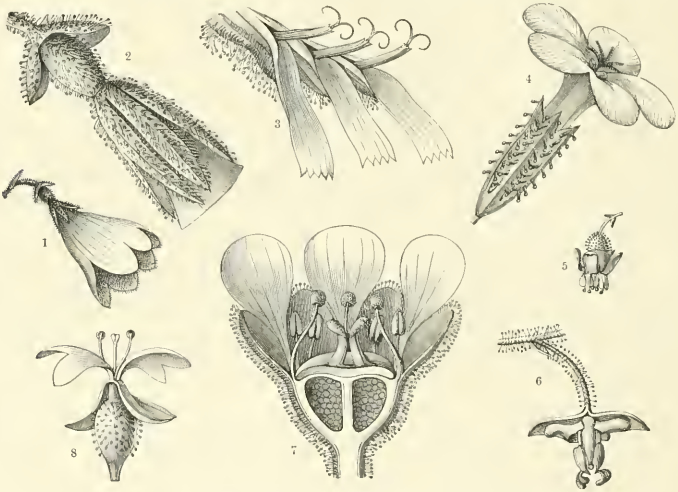


Fig. 261.—Sticky glands as a protection to Flowers.

^{1} Flower of *Linnæa borealis.* ^{2} Calyx, inferior ovary and bracteoles of *Linnæa* (considerably enlarged). ^{3} Three ligulate florets from the capitulum of *Crepis paludosa* showing the glandular scales of the involucre immediately below them. ^{4} Flower of *Plumbago europæa*; the ribs of the calyx are provided with stalked sticky glands. ^{5} Flower of *Ribes Grossularia*; stalked glands shown on the inferior ovary. ^{6} Flower of *Epimedium alpinum;* the pedicel is glandular. ^{7} Section of flower of *Saxifraga controversa* with sticky glands on pedicel, ovary, and calyx. ^{8} Flower of *Circæa alpina* with inferior ovary covered with glands. ^{5} natural size; all the other figures magnified.

In addition to these plants, provided with adhesive glands about the flower and its accessory structures, others exist in which the whole of the foliage is sticky. As examples may be mentioned various Primulas (*Primula glutinosa, viscosa, villosa*), Saxifrages (*Saxifraga controversa* and *tridactylites*), Crassulaceæ (*Sedum villosum, Sempervivum montanum*), and several Steppe-plants (*Cleome* *ornithopodioides*, *Bouchea coluteoides*, &c.). That their stickiness saves the flowers of these plants from many undesirable visitors there can be no doubt. Often enough the dead bodies of small creatures that have ventured upon them may be seen adhering to the foliage. In some of them the plant actually supplements its normal nutrition by a diet of these insects' bodies, and the glandular hairs would appear to subserve the same functions as the similar structures in *Drosophyllum lusitanicum*, and the various species of Sundew and Butterwort already described (*cf.* vol. i. pp. 153–156).

This is the place to mention the waxy coatings of flowering axes and pedicels, which, in a number of plants, guard the flowers from the approach of small creeping insects—though, of course, in many cases they serve another function. The bloom on the catkin-bearing twigs of the Violet Willow (*Salix daphnoides*) and Caspian Willow (*Salix pruinosa*) undoubtedly plays this part. For these Willows, which are diœcious and largely dependent upon bees for the transfer of their pollen, it is of importance that the honey should be reserved for useful visitors and not needlessly wasted. Ants and the like, climbing up to the catkins and attempting to traverse the wax-covered twigs, slip and lose their footing, and tumble down to the ground again.

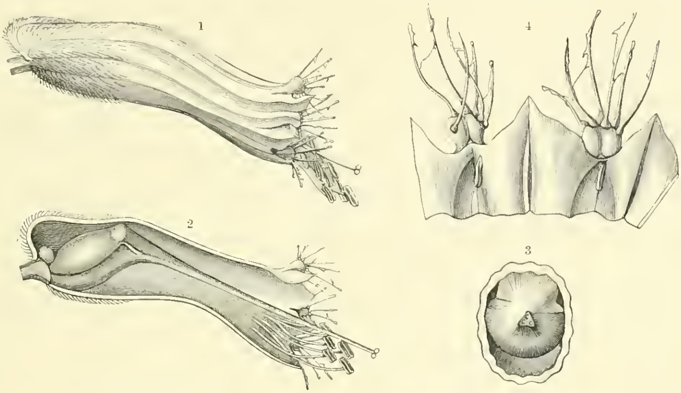


Fig. 262.—Sticky Bristles at the edge of the Calyx as a protection to Flowers.

1 Flower of *Cuphea micropetala*. 2 Longitudinal section of the same flower. 3 Transverse section of the same flower at the height of the insertion of the style upon the ovary. 4 Small portion of the calyx-limb showing the sticky bristles in little tufts. 1, 2, 3 × 2; 4 × 8.

It is not improbable, though no observations are to hand, that the stems and branches of *Melianthus*, *Dentaria*, *Sanguinaria*, *Fritillaria*, &c., by their slippery coating of wax provide a similar protection to the flowers which are rich in honey in each case.

It is especially hard chitinous insects, such as ants, whose progress is arrested by sticky or waxy surfaces in the neighbourhood of the flower. Against snails and slugs such arrangements are less efficacious. Indeed, these creatures are but little incommoded by adhesive secretions, for they can overcome any obstacles of the kind by themselves secreting a copious slime. Towards spines, prickles and stiff bristles, snails, and indeed all soft-bodied animals are extremely sensitive. Thus whilst ants and the like can travel unimpeded over the rough leaves and prickly heads of Teasels, the soft-bodied organisms avoid hispid and spinose surfaces. Stiff bristles teeth, and prickles, then, situated in the neighbourhood of the flowers, form a good protection against visitors of this class. It should be mentioned that these animals —snails and caterpillars—do not take especially honey or pollen, but devour indifferently the petals, stamens, and carpels. It is hardly necessary to describe these spiny mechanisms in detail here, as the subject has been already treated for the case of foliage (vol. i. p. 433), and the two phenomena have very much in common. Two features, however, may be pointed out as having a direct bearing on the matter in hand; firstly, where flowers as well as foliage are protected by spiny structures against creeping animals, the number of these structures increases markedly in the neighbourhood of the flowers; secondly, it often happens that spines placed immediately about the flower serve not only to exclude the unbidden guest, but at the same time as "path-finders" to direct the welcome honey-sucking insect, so that it shall dislodge the pollen and disturb the stigma.

This latter feature applies in marked degree to the sheathing bract-like investments of many flowers which must be surmounted by insects before they can reach the honey. The small capitate flowers of Composites, Scabiouses, and many Pinks are very rich in honey; but this honey is only for insects which visit the flower from above, where the stamens and stigmas are displayed. The illegitimate removal of honey—from below or from the side—must be prevented. Now many insects, especially bees and humble-bees, when they come across honey inclosed in a delicate sheath bite through the wall and steal the honey, as it were, through a back-door. Liability to this class of pilfering must be excluded by tough, impenetrable sheathing structures around the basal, honey-containing regions of the flower. Such structures are well shown on the Teasel-heads and capitula of many Pinks, in which the nectariferous portions of the flowers are protected by imbricating scales. The strongest humble-bee cannot pierce them, and the only alternative is to obtain the honey in the legitimate manner.

It is very generally assumed, and in several cases on adequate grounds, that the inflated calyces and sheaths of bracts which inclose the flowers of many plants serve to protect the honey from marauding of the kind indicated. Thus, in a case in which the honey is distant 20 millimetres from the wall of an inflated calyx, it cannot be reached by the humble-bee whose proboscis is only 8 millimetres long by means of a hole bitten in the calyx. Humble-bees will visit the flower by the ordinary way and get the honey thus with less expenditure of energy. But such relations do not generally obtain; in a majority of cases the interval between the inflated calyx, and the honey is less than 8 millimetres, so that the average humble-bee could get the honey by biting through. As a matter of fact, however, it is usually easier for the bee to get the honey in the ordinary way, and these arrangements of inflated calyces are rather of the nature of protections against creeping insects, ants, and the like than humble-bees. There are in the European Flora some 300 plants whose flowers are robbed by humble-bees biting through the calyx or corolla. For several of them, which depend entirely upon insects for the transfer of their pollen, this burglarious proceeding is fatal. Fertilization is not accomplished; their ovules atrophy and propagation by seed is impossible. Such plants have flowered in vain. Herein lies a contradiction to the otherwise marvellous harmony which exists between the configuration of plants and animals, a contradiction only explicable on the assumption that these plants, whose honey is taken without concurrent pollination, date back to a time at which humble-bees were absent from the district in question. A Catchfly (*Silene Pumilio*), the flowers of which are industriously visited by humble-bees, occurs in the Eastern Alps (Taurus). The great majority of these bees decline to enter the flowers properly, but, hanging on to the inflated calyx, bite a hole in it and take the honey. The Catchfly rarely sets seeds, and one may see hundreds of plants together, not one of which has ripened a fruit, although they flowered freely during the summer. At the present time this Catchfly has a very restricted distribution in the Alps, and even in districts where it occurs is sporadic. Nor does it propagate with any vitality. The same is the case with another Catchfly (*Silene Elizabethæ*, of the Southern Alps) and with several species of Aconite and Corydalis. Any one familiar with the facts, although he may not be an enthusiastic supporter of current hypotheses as to the history of the vegetable world, must admit:—(1) That these endemic species are becoming extinct in the Alps. (2) That the humble-bees are to blame for this in that they steal the honey without doing the plants any service in return. (3) That these plants date back to a time at which humble-bees did not frequent the regions where they grow, and at which the flowers needed protection only from creeping insects.

The bulk of the arrangements, so far described for the exclusion of unbidden guests, occur outside the cavity of the flower, and are directed against creeping animals which climb up from the ground. Those, on the other hand, directed against undesirable winged-insects are situated chiefly *inside* the flower and take the form of hairs and fringes. These may be arranged either into irregular tufts and woolly plugs, or with greater regularity, into lattice-works, cages, and crowns of hairs. Thus we find a woolly thicket occupying the whole cavity of many bell-shaped and urceolate corollas, as in the Bearberries (*Arctostaphylos alpina* and *Uva-ursi*, fig. 263 [1]), or the hairs are confined to the tubular portion of the corolla as in the little alpine *Primula minima*. In the Alpine Roses (*Rhododendron hirsutum* and *ferrugineum*) and in several of the Honeysuckles (*Lonicera nigra*, *Xylosteum*, and *alpigena*, fig. 263 [7]), the stamen-filaments and parts of the corolla contribute hairs, which, in the aggregate, make a thicket defending the honey. Often the corolla is quite smooth inside, and the bases of the stamens alone are provided with flocks of hair which screen the nectaries, as in *Atropa*, *Lycium*, and *Polemonium*. In the well-known climber *Cobæa scandens*, the insertion of each stamen is inclosed in a regular felt, and these five felty tufts form, as it were, a sort of diaphragm which cuts off the honey-secreting, basal region of the flower from the main cavity of the bell (see fig. 263^{5}). Again, in the Tulip (fig. 263^{4}), each stamen secretes honey at its base in a little depression of the filament on the side directed towards the perianth. Tufted hairs completely cover the nectary, so that insects have to lift the whole stamen to get honey. In *Daphne Blagayana* (fig. 263^{6}) the stalked ovary is enveloped in hairs, by which the honey formed at the base of the flower is protected from unbidden guests.

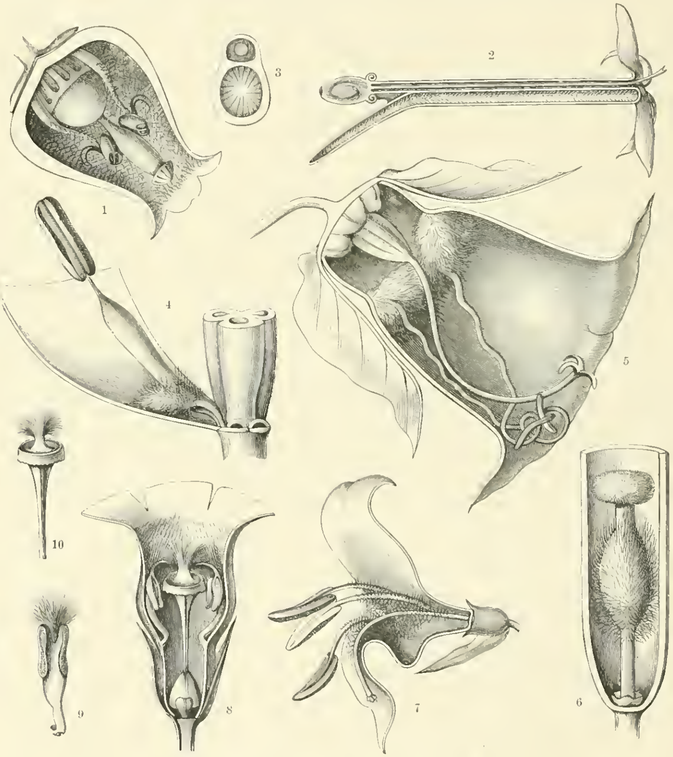


Fig. 263.—Tufts of Hair as a Protection to Flowers.

[1] Longitudinal section of the flower of the Bearberry (*Arctostaphylos Uva-ursi*). [2] Longitudinal section of flower of Red Valerian (*Centranthus ruber*) [3] Transverse section of the same flower. [4] Portion of the flower of *Tulipa sylvestris* [5] Longitudinal section of flower of *Cobæa scandens*. [6] Longitudinal section of flower of *Daphne Blagayana*. [7] Longitudinal section of flower of *Lonicera alpigena*. [8] Longitudinal section of flower of *Vinca herbacea*. [9] Single stamen of *Vinca*. [10] Style and stigma of *Vinca*. [5] Natural size. All the other figs. magnified.

In the flowers of *Vinca herbacea*, indigenous to the Steppes of the Black Sea (*cf.* figs. 263 [8, 9, 10]), the apices of both stamens and stigma are provided with tufts of hairs which interlock and close the mouth of the corolla-tube, as it were, with a plug of cotton-wool. One of the most curious of these arrangements is found in the Red Valerian (*Centranthus ruber*, fig. 263 [2]). The corolla-tube is some 12 millimetres long and scarcely 1 millimetre in diameter; it is divided longitudinally by a membraneous diaphragm into two tubes, of which the upper contains the long style, whilst the lower one, produced into a spur, contains the honey. This lower tube is lined throughout its entire length with hairs, which, although they present no obstacle to the introduction of a proboscis, prevent little insects from creeping in and stealing the honey. As may be seen in fig. 263 [3], these hairs project a considerable distance into the interior of the tube.

Hedges or palisades of erect elastic hairs or fringes, inserted on circular cushions in tubular corollas, are not infrequently met with. These fringes stand straight out into the tube and conceal its cavity. They are sometimes quite at the mouth of the tube, as in *Veronica officinalis*, sometimes a little distance down the throat, as in the Vervain (*Verbena officinalis*), or quite at the base, as in *Acanthus*, *Phlox*, *Horminum*, and *Prunella*. Fringed scales in rings are found in the flowers of many Genetians and Passion-flowers. In several Rutaceæ, *Haplophyllum*, for instance, hairs from the bases of the stamens form a sort of lattice-work at the base of the flower, whilst, in a species of *Monotropa*, the cushion beneath the stigma bears radiating hairs which, reaching as far as the corolla, make an elegant grating. The honey in *Swertia perennis* is secreted in little cup-like depressions near the bases of the petals. The margins of the cups are fringed with hairs which converge, and are so interwoven that the cups are protected by little cages. These few examples are typical of a vast series of lattices, gratings, and the like, occurring in flowers to shield the honey.

Protection from undesirable visitors is also obtained in a great variety of ways by the bending, twisting, or convergence of various parts of the flower, so that the honey is hidden in grooves and special cavities. Amongst these are included flowers with long, narrow tubes, into which the delicate proboscis of a butterfly can be introduced, but which are too narrow for small insects to crawl into; also, such as have various projections, cushions, and lobes of the corolla which narrow or subdivide the aperture; finally, closed flowers which can only be opened by powerful insects, and such as have their stamens so crowded that little insects cannot obtain access to the honey. Several of these have been already described and figured (p. 180, 181).

We may also regard the periodic display of attractions to insects as being, in a way, of the nature of a protection against unbidden guests. The subject has been already alluded to (p. 156) in detail, so we need only add that the arrangements obtaining in many moth-visited Caryophyllaceæ are also found in *Zaluzianskia lychnidea*, a Scrophularineous plant from the Cape. Its flowers have a long honey-secreting tube and spreading limb (as in *Silene*), the ten lobes of which are dark purple underneath and brilliant white above. By day the lobes are furled, so that their dark inconspicuous sides are shown, nor is there any scent or other attraction; consequently it remains unnoticed by day-flying insects. But in the evening the lobes of the corolla fold back, and the white flowers are now conspicuous, whilst a strong Ylang perfume is given off to attract moths. In *Hesperis tristis, Pelargonium atrum* and *triste,* there is a similar periodic exhalation of perfume, though the inconspicuous petals always remain in one position. But here the scent is the main attraction, and at nightfall numerous moths are attracted by the delicious perfume of Hyacinths which is then apparent. *Hesperis* is visited by great numbers of Owlet-moths (Noctuæ) of the genus *Plusia,* which transfer the pollen from flower to flower.

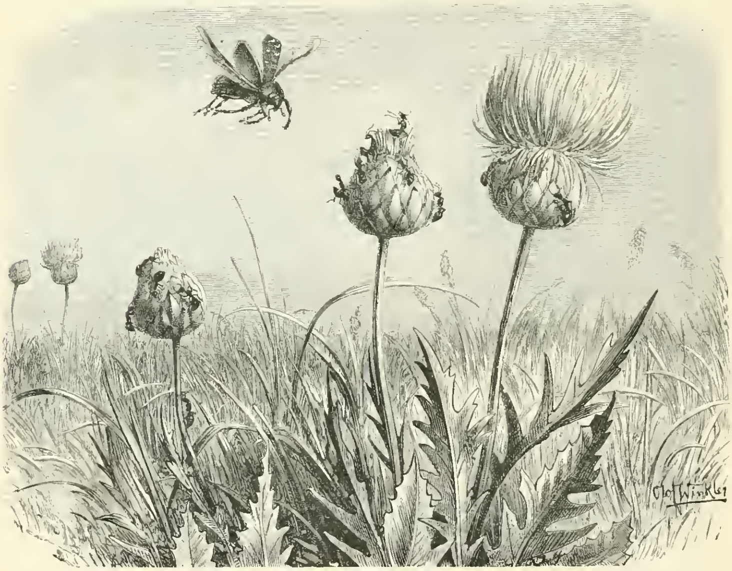


Fig. 264.—Capitula of *Serratula lycopifolia* protected by Ants (*Formica exsecta*) from the attacks of a Beetle (*Oxythyrea funesta*).

Silene nutans, already so fully described (p. 154), may be regarded as the type of the plants now under consideration. It is additionally interesting in that it possesses a double protection against unbidden guests. By its unattractive character during the daytime it is protected from diurnal flying insects, whilst the sticky secretion on its flowering axis keeps off crawling animals such as ants.

So much has been said in this chapter concerning ants as undesirable visitors, and of the means for their exclusion, that this is an appropriate place for a brief account of certain instances in which they are of real service in guarding and protecting flowers. We have already seen how ants are diverted from visiting flowers by honey secreted on the foliage, and how, in certain instances, an actual symbiosis obtains between the plant and the ants. Especially do these ants protect the foliage from the attacks of leaf-eating animals. This reciprocal service, performed by the ants, is in no wise of the nature of gratuitous philanthropy, it is done in their own interests. The lodging and the food which the ants obtain from the plant constitute two of their most important necessities, consequently it is worth their while to protect the "goose that lays the golden eggs".

A similar state of affairs is met with on the capitula of several Composites indigenous to South-eastern Europe, e.g. *Centaurea alpina* and *Ruthenica*, *Jurinea mollis*, and *Serratula lycopifolia*—the last of which is figured opposite. The young capitula of these Composites are particularly liable to the attacks of devouring beetles, especially of *Oxythyrea funesta*, which bites big holes in the heads, destroying crowded flower-buds and involucral scales without the least difficulty. To meet this danger a garrison of warlike ants is employed. Honey is secreted from big stomata on the imbricating scales of the still-closed capitula in such quantities that one can see a drop of it on every scale in the early morning, whilst later in the day, as the water evaporates, little masses, or even crystals of sugar are to be found. This sugar, either in its liquid or solid form, is very palatable to the ants, which habitually resort to these capitula during the period of its secretion. And to preserve it for themselves they resent any invasion from outside. If one of the aforementioned beetles appears they assume a menacing attitude. They hold on to the involucral scales with their last pair of legs and present their fore-legs, abdomen, and powerful jaws to the enemy, as shown in fig. 264. Thus they remain till the beetle withdraws, if necessary hastening its retreat by squirting formic acid in its direction. Then they quietly begin to feed on the honey again. Ants of the same species do not fight amongst themselves on these Composites, although as many as ten to fifteen specimens of the ant *Camponotus Æthiops* live on each capitulum of *Jurinea mollis*, and about the same number of *Formica exsecta* on the heads of *Serratula lycopifolia*.

As soon as the florets on the heads begin to open, the secretion of honey diminishes and ultimately ceases. No longer do beetles come to devour them, nor is there any further need for protection. The garrison is withdrawn, the ants going away in search of other, younger flower-heads.

TAKING UP OF POLLEN BY INSECTS.

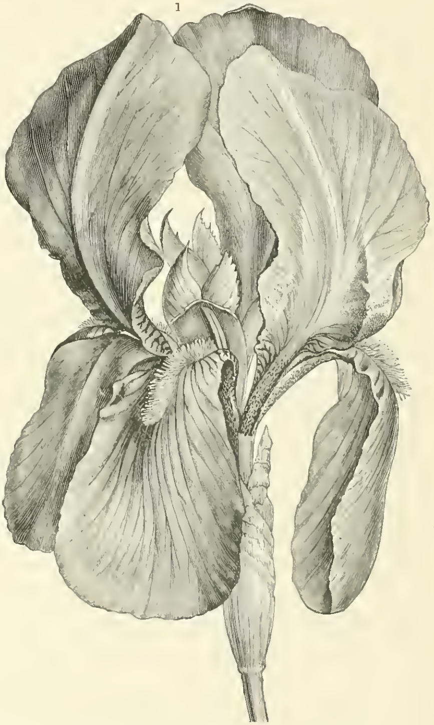
Having obtained in the last chapter a general survey of the contrivances in connection with the advent and reception of insects at the portals of flowers, we are now in a position to describe the means whereby insects, after reaching the flowers, are covered with the pollen there awaiting them.

The simplest case is that where the insects rove and climb about the flowers, and so get powdered all over with pollen. This happens in innumerable Umbelliferæ, Dipsaceæ, and Caryophyllaceæ, which, owing to the association of large numbers of flowers in umbels, fascicles, spikes, or capitula, afford a playground richly furnished with slender waving stamens where pollen is easily to be shaken or brushed off the anthers on every hand, although each single blossom only contains a few stamens. In the case, too, of the single flowers of Roses, Anemones, Peonies, Poppies, Magnolias and Opuntias, which are well supplied with stamens, insects pushing between the anthers or feasting on pollen that has dropped upon the petals get covered on head, thorax, abdomen, wings, and legs with the floury pollen. This is true also of the spathes of Aroideæ and of fig-inflorescences which are haunted by midges, beetles, and gall-wasps, and deposit their pollen on these visitors as they crawl out of their temporary refuge in the manner described on pages 156–160. Mention was made in the same chapter of the fact that insects, after being imprisoned for a time in the flowers of the *Aristolochia*, are quite covered with pollen when they emerge. The phenomenon, which was there merely glanced at, is so remarkable that it is worth while to give a somewhat fuller account of it. In the widely-distributed species of Birthwort represented in fig. 257 [8] on p. 226, and named *Aristolochia Clematitis*, the way into the enlarged base of the flower is over a convenient ligulate alighting-place and through a dark and comparatively narrow passage lined with hairs. The free extremities of these hairs point inwards, *i.e.* towards the inflated chamber, and they permit visitors from the insect-world—small black midges of the genera *Ceratopogon* and *Chironomus*—to pass into the chamber. But once inside, the midges are obliged to reconcile themselves to remaining imprisoned for a couple of days. The hairs, whilst offering no hindrance to ingress present a bristling stockade of points to insects seeking to escape (see fig. 257 [9]). At first the midges endure their captivity with complacence, for the warmth of their dungeon suits them, whilst the succulent cells lining its walls afford a certain amount of nutriment. On the second or third day of imprisonment the lateral walls of the anthers, which are adnate to the stigmatic column, open and let the mealy pollen fall to the bottom of the chamber. The pollen is also acceptable to the midges for food, and they feast upon it liberally. At last, however, they become restless and look for a means of exit, and in bustling actively about the chamber, they cover their entire bodies with pollen. After this the hour of their deliverance is no longer deferred. The hairs in the narrow passage wither and collapse, leaving a free exit, and the midges all be-powdered with pollen hasten to leave the flowers. That they retain no unpleasant recollection of their temporary confinement may be inferred from the fact that they have no sooner escaped from one flower than they creep into another, which has only just reached the stage at which entrance becomes possible. This latter circumstance must be emphasized in order to arrive at a complete understanding of the significance of the curious phenomenon just described. The moment the flower is accessible to insects, the stigma is ready to receive the pollen whilst the anthers are still closed. When the midges proceed from an older to a younger flower, they brush against the latter's stigma, which is situated right in front of the inner end of the dark passage, and deposit the pollen they have brought with them upon it, and may thus bring about cross-pollination between the different flowers.

In many cases insects visiting the interiors of flowers only get smeared with pollen on the upper or the under parts of their bodies, or at particular spots merely, and the adherence of the pollen ensues on their rubbing against the anthers which are situated along the insect's route when it enters or leaves the flower. This process takes place in a great variety of ways. In one case, the only part dusted with pollen is the proboscis; in another, the head; in a third, the shoulders or back; in a fourth, the upper surface of the abdomen; in a fifth, the under surface of the abdomen. There are instances also in which the pollen is only brushed off by the peculiar collecting-brushes on the legs of bees which were spoken of in the last chapter. Again, reference was made on page 153 to the remarkable case of the small moth *Pronuba yuccasella*, which has the first joint of its maxillary palp metamorphosed into an organ of seizure, and by means of that implement collects the pollen from *Yucca*-flowers, makes it up into a ball and holds it fast in front of its body (see fig. 240 [5], p. 157).

If stamens, projecting out of the flower or situated on the floral threshold, serve as a place for insects to alight on, as, for instance, in the flowers of Funkia, Viper's Bugloss, Figwort and Monkshood (*Funkia, Echium, Scrophularia, Aconitum*), pollen adheres to the underneath part of the insect's body the moment it settles, or as it crawls towards the interior of the flower. In one of the species of Alpine Rose (*Rhododendron Chamæcistus*) and in the Germander Speedwell (*Veronica Chamædrys*; see fig. 257 [1], p. 226), insects visiting the flowers, which are directed laterally, grasp the exserted stamens with their front legs as if they were perches. The stamens are arranged so as to bend downwards and inwards when touched, thus they become almost instantaneously applied to the under surface of the insect's body, which becomes smeared with the pollen. Great quantities of pollen adhere to the under parts of insects in the case of Composite inflorescences. Shortly after the opening of the corollas, the style bearing an external load of pollen is exserted from each of the little tubular and ligulate florets composing the capitulum in this group, and, owing to the fact that large numbers of these florets invariably open simultaneously, numbers of styles laden with pollen project close together from the discoid head. A largish insect settling on a capitulum may therefore be dusted with the pollen of numerous florets at once. As he twists and turns about on the disc of the inflorescence inserting his proboscis into one floret after another a lot more pollen is brushed off on to the under surface of his body, and he finally leaves the capitulum with an abundant freight.

The transference of pollen to insects takes place in the Lady's Slipper Orchid (*Cypripedium*) in a manner altogether peculiar. Here it is only one of the shoulders of the visitor that receives the pollen. We will briefly describe how this happens in the case of the European species (*Cypripedium Calceolus*). The floral envelope of this Orchid (see fig. 267 [1]) consists of six leaves, one of which is shaped like a slipper, and has its deep cavity furnished at the bottom with hairs full of sap. Sometimes little drops of nectar are also secreted by the cells composing these hairs. Certain small bees of the genus *Andrena* are in the habit of entering the cavity to feast on the hairs. Three ways are open to them, viz. the two small orifices in the background on either side of, and close to, the column, and the large oval opening in the middle of the slipper and in front of the column. They choose the last and slip under the broad, rough stigma to the bottom of the slipper where they feed on the succulent cells of the hairs. After a time they wish to escape into the open air again, but that is not so easy. The edges of the large central opening are inflected (see fig. 267 ²), and so fashioned as to be unscalable, and the bees have no choice but to make use of one of the two little exits at the back of the slipper. Even through these escape is not altogether easy, the bees being obliged to squeeze through the narrow opening. The result is that one shoulder brushes against the soft, viscid pollen of the anther which forms the inner border of the orifice. The last act in the story is the entrance of the insect with its shoulder covered with pollen into another *Cypripedium* flower, whose rough stigma is thereupon immediately besmeared with pollen.



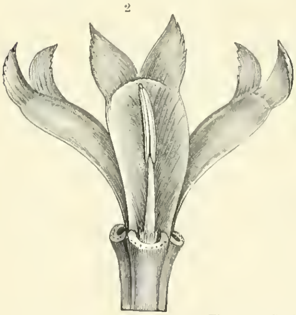


Fig. 265.--Contrivances for loading insects with pollen.

¹ Flower of an Iris (*Iris Germanica*), with three segments of the perianth reflexed and three erect. On each of the former is a strip of yellow hairs which stand out conspicuously from the violet background of the perianth-segment, and serves as a guide to insects entering the honey-containing tube of the perianth. ² Upper half of the perianth-tube showing the three passages leading to the honey. Above each passage is a stamen with a long, linear anther facing outwards, and arching over each stamen is one of the three bi-lobed petaloid stigmas. The perianth-lobes have been removed.

Instances are very common in which insects in seeking honey brush the upper parts of their bodies against the anthers, thus covering their backs with pollen. Humble-bees, when they visit Iris flowers (fig. 265), settle on the hairy ridges of the outer deflexed perianth-segments as the most convenient alighting-places, and thence proceed to the honey-containing canals of the perianth-tube. They thus pass under one of the petaloid stigmas, and at the same time under the corresponding stamen, which is so placed and curved as to exactly fit the dorsal surface of the humble-bee. The pollen is thus brushed off on to the insect's back. Similarly, bees entering the gaping flowers of *Gladiolus*, of the Dead Nettle (*Lamium*) and other Labiates rub their backs against the anthers, which are concealed close underneath the upper lips, and carry away pollen on that part of their bodies only. The same holds good in the case of the humble-bees which slip into the large bells of Gloxinia, clamber up to the honey in Foxglove flowers (*Digitalis*), or venture into the jaws of the Snapdragon or Toad-flax (*Antirrhinum, Linaria*). In the flowers of *Linaria* two pairs of large anthers are situated close under the arch of the upper lip, and the pollen discharged by them is in the form of two round balls, which are both detached at once from the fissures in the anthers upon the occasion of an insect's visit, and are carried away to other flowers on the back of the intruder.

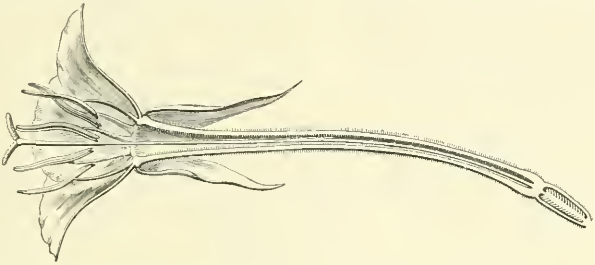


Fig. 266.—Longitudinal section through a flower of the Evening Primrose (*Œnothera biennis*).

The laterally-directed flowers of the Evening Primrose (*Œnothera*; see fig. 266) are visited by moths which insert their probosces into the long floral tubes as they flutter about in front of the flowers. In so doing, the moths brush their heads against the anthers surrounding the entrance to the flower-tubes, and cover them with pollen. The head is also the part affected in the case of the Sun-birds (*Cinnyridæ*) which take the rich brown honey from the lower, bowl-shaped sepal of *Melianthus* flowers (see fig. 258 [12], p. 227), and in the process bring their heads into contact with the anthers above it.

The adaptation of flowers with a view to ensuring that insects seeking their honey shall brush off the pollen with some part of their bodies, whether back, belly, shoulders, head, or at least the proboscis, is of so manifold a character that it is impossible, having regard to the scope of the present work, to deal with all the contrivances coming under this category. Only a few of the most striking examples will be described, and as they are to a certain extent identical with those already referred to in connection with the subject of the protection of honey, we need not enter into them at so great length as would otherwise be necessary. In the first place, there are the flowers which are furnished inside with prickles or sharp, stiff bristles. It is well known that honey-sucking insects, such as humble-bees, are very careful of their probosces, keeping them in special grooves in their bodies whenever they are not in use, and taking pains when they do use them not to thrust them against rigid points on account of their liability to injury. Thus a flower, furnished with sharp prickles or bristles, only admits an insect's proboscis by a well-defined path. The intruder avoids the points, and is thereby prevented from entering by a route which would not involve its rubbing against the anthers —and is induced to take a course inevitably accompanied by the deposition of pollen on its back, head, or proboscis. This occurs, for instance, in some Cruciferæ (*Braya alpina*, *Malcolmia Africana*; see fig. 267 [6]), where the insects are guided to the honey between two series of rigid upright bristles borne by the ovary, and are obliged to brush their heads and probosces against the pollen-laden anthers. The same thing happens in *Leonurus heterophyllus* (see fig. 267 [7]), a Labiate, which has a patch of sharp prickles in the throat just behind the under-lip. Insects desirous of possessing the honey secreted at the base of the flower, and at the same time of avoiding the prickles, are obliged to insert their probosces close under the upper-lip, and are thus brought into contact with the pollen-covered anthers there situated. In several small alpine Gentians, such as *Gentiana glacialis* and *G. nana*, the entrance to the interior of the flower is covered by four valves with lacerated margins which are so pliable as to form no barrier to the entrance of the stronger kinds of insect. But no anthers would be brushed by their probosces if they were to enter by that way, and the possibility of such an occurrence must, therefore, be obviated. The fringed edges of the valves closing the throat are for this purpose thickly studded with minute prickles. Insects reject the route as too risky and prefer to enter between the points of insertion of the valves whence passages of adequate size and quite free from danger lead to the honey. In passing along them the insects brush the anthers which are situated close by. The compulsory condition imposed on insect-visitors that they should rub the pollen off with their probosces, and occasionally with the tops of their heads and front parts of their thoraces, depends in many cases on the fact that there is only one approach leading to the honey, and the external orifice of this passage is straitened by a ring-like callosity, or by the presence of flaps or scales, whilst the anthers are situated round the orifice, or just underneath it. This arrangement is found, for example, in many Boragineæ, Oleaceæ, Primulaceæ, and Polemoniaceæ. The hawk-moth, which sucks honey in the autumn from the flowers of the Phlox, a plant belonging to the Polemoniaceæ, and butterflies, which feast in the spring on the sweet juices of Lilac-flowers load only their probosces with pollen, for, in consequence of the form and disposition of the various parts of the flowers, this part alone comes into contact with the anthers.

The same mechanism exists in so-called "revolver-flowers," *i.e.* flowers which exhibit within their outer portals the open ends of a number of small tubes resembling the barrels of a revolver. These tubes are arranged in a great variety of ways. In Bindweeds and Gentians (*Convolvulus, Gentiana*) the filaments are adnate to the corolla-tube and project in the form of ridges towards the central ovary, and so divide the main tube into four or five separate pipes. In some Geraniums and several species of Flax (e.g. *Geranium Robertianum, Linum viscosum*), a ridge arises from the middle of each petal and projects towards the centre of the corolla, dividing it into five tubes, which surround the styles and stamens in a circle. In Flaxes of the group *Cathartolinum* each petal is swollen in the middle and attenuated, and concave near the edges; the juncture of the concave margins of adjacent petals gives rise to a flat canal which leads to the floral receptacle. The corolla-tube of the Winter Cherry (*Physalis*) is fluted by five grooves, which, together with the villous filaments facing them, form as many tubes. In all these

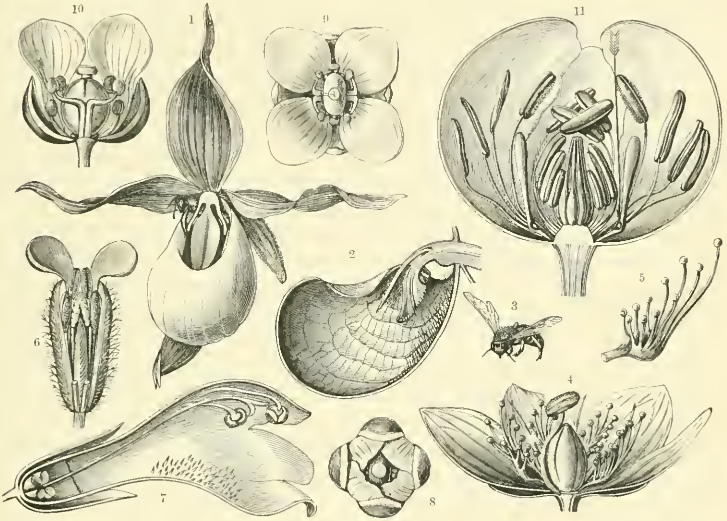


Fig. 267.—Contrivances for ensuring the deposition of pollen on insect-visitors.

[1] Flower of the European species of Lady's Slipper (*Cypripedium Calceolus*). A bee (*Andrena*) is forcing its way out through one of the holes at the side of the stigma and smearing its shoulder with pollen. [2] Longitudinal section through the labellum and column of the Lady's Slipper. [3] An *Andrena* on the wing. [4] Flower of Grass of Parnassus (*Parnassia palustris*) with the front sepals, petals, nectaries, and stamens cut away; of the stamens which are visible three are despoiled of their anthers, the fourth has assumed a position placing the anther in the middle of the flower. [5] Single nectariferous scale from the flower of *Parnassia*. [6] Flower of *Malcolmia maritima* with the front sepal, the two front petals, and two stamens cut away; the visible portion of the ovary bearing a longitudinal row of stiff bristles (white). [7] Longitudinal section through the flower of *Leonurus heterophyllus*. [8] Flower of *Kernera saxatilis* in the first stage of development, seen from above. [9] The same at a later stage of development, seen from above. [10] The same flower, seen from the side, with the front sepal and the two front petals removed. [11] Vertical section through a flower of *Trollius Europæus* (Globe-flower). [1] and [2] nat. size; the rest × 2–8.

"revolver-flowers" the anthers are so placed with their pollen-covered faces in front of the mouths of the tubes, that insects inserting their probosces are bound to rub against them.

The flowers of the Wild Mustard (*Sinapis arvensis*), *Diplotaxis*, and several other Cruciferous plants have anthers, which, after dehiscence, execute spiral twistings with the object of turning the face covered with pollen away from the stigma, and placing it near the spot where insects insert their probosces for the honey. In other Cruciferæ, with flowers somewhat resembling "revolver-flowers" in structure, although the approach to the honey is not straight through a tube, the stamens exhibit characteristic bendings of the filaments with a view to bringing the anthers into the line of entrance to the nectar. Thus, for instance, in the flowers of *Kernera saxatilis* (see figs. 267 [8, 9, 10]), honey is only to be found on the two narrow sides of the compressed ovary, although there are petals all round the ovary. Supposing all the filiform filaments, whether in front of the narrow or of the broad sides of the ovary grew straight up, only the anthers borne on the former would deposit their pollen on the honey-sucking insects. In order to render the anthers situated opposite either of the broad sides of the ovary which are destitute of honey liable to be stroked by intruding insects, their filaments are bent at right angles, as is shown in figs. 267 [9] and 267 [10]. By this means all the dehiscent anthers of the flower are brought into such a position as to be necessarily rubbed by insects when they come to suck the honey. Movements of stamens, directed to the same end, are also observed in numerous Caryophyllaceæ, Ranunculaceæ, Saxifrageæ, Crassulaceæ, and Droseraceæ. The floral structure in the Caryophyllaceous plants coming under this category is similar to that of "revolver-flowers"; the petals are unguiculate, that is to say, they are composed of an inferior very narrow part inserted in the tubular calyx, called the claw or *unguis*, and a flat expanded region above the calyx called the *lamina*. A groove runs down the middle of the claw to the floral receptacle, and at the upper end of the groove, where butterflies are to introduce their probosces, the lamina is sprinkled with bright-coloured patches or speckles, and is furnished sometimes with scales arranged in pairs, or something else of the kind to make the entrance conspicuous, and regulate and facilitate the introduction of the proboscis. In these Caryophyllaceæ the anthers, just after dehiscence, are so placed in relation to the entrance that butterflies must necessarily smear their heads and probosces with pollen as they thrust the latter organ along the grooves. After that has happened, the filaments bend to one side or stoop down beneath the laminæ of the petals, and then other stamens come into play, their anthers being held, as the first were, in front of the grooves running down the petals. In the Ranunculaceæ—*Eranthis, Helleborus, Isopyrum, Nigella, Trollius* (see fig. 267 [11])—a large number of stamens surround the central multiple pistil in several whorls. They are themselves encompassed by a circle of very small trumpet-shaped or tubular petals filled with honey, the so-called nectaries, and these are in their turn surrounded by large floral leaves, white, yellow, red, or blue in colour, which descriptive Botanists have designated as petaloid sepals. Shortly after the interior of the flower becomes accessible, owing to the opening of these sepals, the anthers belonging to the outermost whorl of stamens dehisce. Their filiform filaments have in the meantime undergone elongation, inflection, and torsion to the extent necessary to bring the anthers exactly over the opening admitting to the little cups full of honey. Insects cannot suck the honey without brushing against these anthers. The next day the stamens of the first whorl move in an outward direction towards the sepals, their place being at once taken by the stamens of the next whorl nearer the centre of the flower. By the third day these, too, are reflexed and replaced by the members of the third whorl; and the process continues until all the stamens in turn have set their anthers over the nectaries. The punctuality and exactitude with which the whole series of operations is carried out is most extraordinary.

The same phenomenon may be observed in the flowers of the Grass of Parnassus (*Parnassia palustris*). Only here the number of stamens is limited to five, and one anther at a time is set in the way of alighting insects as is shown in fig. 267 [4]. The honey is secreted in two small oblong depressions on the inner face of certain curious fimbriate leaf-structures which are inserted between petals and stamens (267 [5]). If an insect in search of honey alights from above on the middle of the flower, it is certain to brush its proboscis against the particular anther which has set free its pollen that very day, and is itself in close proximity to the approach to the honey. The Grass of Parnassus possesses in addition another extremely interesting contrivance correlated with the movements of those insects, which, instead of alighting from above, settle on the edges of the petals. When such an insect moves from the margin of the expanded petals towards the nectaries it encounters a barrier in the form of railings composed of the radiating arms of the nectariferous scales. This barrier is not, however, insurmountable; its radiating arms do not secrete any viscid substance or terminate in sharp points, but are surmounted by round yellow knobs, resembling pins' heads (see fig. 267 [5]). The insect easily climbs over this obstacle without hurting itself, and then finds itself on the side of the scale where the nectaries are. But in doing so, it is brought so nearly to the middle of the flower that it is sure to touch the anther, which, having opened that very day, occupies the position commanding the passage to the nectar. We have here an instance of the adaptation of a flower to different visitors. Both those which settle from above and those which crawl from the edges of the petals are obliged to brush against the effective anther in the middle of the flower and besmear themselves with its pollen.

In all these cases the pollen pours in copious quantities from the anthers and forms either puffy masses which cling to the gaping loculi, or else a viscid mantle clothing the slender style, when that organ has been used to sweep it out of a tube of syngenesious anthers. Insects, on visiting the flowers, come into immediate contact with the pollen, it being in no way covered or wrapped up, and being obtruded so directly in the path that to avoid it would be impossible. In the next series of plants there is a certain amount of difference in this respect. The pollen is not accessible direct, but is concealed in tubes or recesses, and the covering must be removed before an insect can be besmeared. In the composite flowers of the genera *Onopordon* and *Centaurea*, to which belongs, amongst others, the well-known Corn-flower (*Centaurea Cyanus*), the anthers are borne on slender filaments, and, as in all Compositæ, are connate into a tube, in which is concealed the upper portion of the style. The dehiscence being introrse, the pollen is deposited on the style. In the majority of Compositæ, the style then grows in length and pushes the pollen up beyond the top of the tube. But this is not the case in *Onopordon* or *Centaurea*. No elongation of the style occurs, and the pollen remains concealed in the tube. If, however, an insect sets foot on the central part of the capitulum and comes into contact with the stamens as it clambers over the florets of the disc, the filaments immediately contract, drawing back the sheathing anther-tube and leaving the pollen exposed on the top of the style, which is then brushed against by the under surface of the insect. The same result is achieved by different means in certain Papilionaceæ. The well-known *Cytisus, Melilotus, Trifolium, Onobrychis* are instances of one group. The front pair of petals, which is known as the keel, and serves as an alighting-place for insects, forms a receptacle with a very narrow opening at the top. In this are concealed the ten stout, partially connate filaments, and the anthers borne by them. When a humble-bee settles on the keel and inserts its proboscis into that part of the flower where honey is to be found, the keel is pressed down by the insect's weight, and the anthers are in consequence exposed, whilst the pollen resting upon them is rubbed off on to the under surface of the insect. The moment the insect leaves the flower the keel springs back to its former position, and once more conceals the anthers which, as a rule, have only parted with a portion of their pollen. The same process is repeated on occasion of each fresh visit, and as many as four different insects may thus be dusted with pollen from the same flower. In *Lathyrus, Orobus, Pisum, Vicia,* the phenomenon is in the main the same, but these plants have a special brush developed in connection with the style which sweeps the pollen out of the keel, where it has been deposited by the anthers, at the same moment as the insect alights on the flower. The insect is thus certain to carry away pollen on the under parts of its body.

The transference of the pollen in the Hemp Nettle (*Galeopsis*) and Monkey-flower (*Mimulus*) to the bodies of insects is also attended by a curious phenomenon. A stamen of *Galeopsis* is shown in fig. 216 [19], p. 91. The corolla is bilabiate, and beneath the arch of the upper lip are two pairs of stamens, one pair behind and the other in front of the stigma, which is bilobed, and has the property of shutting together its two component flaps in response to contact. Each of the anthers of the pair behind the stigma is box-like, and divided by an internal septum into two compartments capped by lids. If a needle is inserted into the flower so as to touch the anthers, the lids spring open, disclosing the pollen, which sticks to the needle; a similar action occurs when an insect visits the flower.

These cases, where the pollen has first to be uncovered by the insect before it can be carried away, are not more remarkable than those wherein pollen-masses are concealed in niches, and are caused to adhere to the bodies of intruding insects by means of a special organ, and are then drawn out of their hiding-places. This method of transferring the pollen is especially characteristic of Orchids, and is extremely interesting. It will be worth while to consider it in some detail in connection with a few well-known instances, and for that purpose it will be necessary to begin with a general description of the peculiar structure of the flower in Orchids. In all species of Orchidaceæ the ovary is inferior, and at the flowering season resembles a pedicel. It bears at the top two tripartite whorls of floral leaves, one standing just above the other. Two segments in each whorl are alike in form, whilst the third is different. The difference is most conspicuous in the case of the odd segment of the inner whorl, and it is called the lip or *labellum*. Often it really resembles a lip, but not uncommonly it assumes the shape of a sabot, boat, or basin, whilst, in other cases, it is like an outstretched tongue, or even the body of a spider or insect (see fig. 257 [2], p. 226 and Plate XIII.). The labellum is frequently lobed, and may also be fringed or slit up into long curling strips. In fact it exhibits an endless variety of configuration, and to it is mainly due the extraordinary appearance characteristic of Orchids. The ovary itself is produced in most Orchids above the two perianth-whorls, and rises up in the middle of the flower as the so-called *column*. This structure, which bears the stamen and the stigmatic surface, is always opposite the labellum, so that the approach to the bottom of the flower lies between the two. There are *two* stamens in the few Orchids allied to the already-mentioned Lady's Slipper (*Cypripedium*; see figs. 267 [1] and 267 [2]), but throughout the others only *one* stamen in each flower develops pollen. The filament can only be identified by careful examination and dissection of the flower; externally it is not visible. Usually the anther or pair of anthers is imbedded in pits or recesses in the column, or is adnate to one face or to the top of the column. In the flowers of the Helleborine (*Epipactis latifolia*, fig. 268 [2]), and many other Orchidaceæ, on either side of the one stamen, which has a fully-developed bilocular anther, may be seen an abortive stamen in the form of a triangular tooth. The column bears, in addition to the stamens, a stigmatic surface corresponding to the tips of the three carpels. In the group of Orchids represented by the Lady's Slipper (*Cypripedium*) all three are capable of taking up pollen; in all other Orchids only two stigmas are receptive, and they are usually merged together into a single disc or plate; the third stigma being transformed into the so-called *rostellum*, a structure which plays an important part in connection with the processes now to be described. The rostellum assumes the most various forms in different Orchids, and special relations subsist between it and the anther. In many cases the rostellum is a beak-like structure, situated betwixt the solitary stamen and the stigmatic surface; it marks, so to speak, the frontier between these two structures. Certain portions of the rostellum disintegrate, forming a tough and extremely sticky mass like bird-lime, which, in most cases, takes the form of a wart. The anther is bilocular. The loculi contain each a clavate pollen-mass or *pollinium*, and open betimes—often indeed, before flower is open. After dehiscence the pollinia may be seen peeping out of the longitudinal slits in the loculi with their narrower extremities connected with the adhesive portion of the rostellum (as in fig. 268 [2]). The manner in which this connection is established varies greatly, according to the species, and cannot be discussed here; all we need note is the fact that the union is so strong that the two pollinia are drawn out of their hiding-places and carried away by any object which, coming into contact with the rostellum, removes the viscid mass from it. The Broad-leaved Helleborine (*Epipactis latifolia*), a plant of wide distribution in Europe, exhibits extremely well all the peculiarities of Orchids above referred to (see figs. 268 [2] and 268 [3]). The upper part of the labellum is excavated, and contains a copious supply of honey. Above the labellum is the quadrangular stigma (fig. 268 [2]) borne by the column, and surmounting this is the wart-like and projecting rostellum (a white dot in the figure), whilst the anther crowns the column. The two pollen-masses developed in the anther are connected with the viscid portion of the rostellum. Fig. 268 [4] shows what the pollinia look like when they are drawn out of the anther. The honey secreted in the cavity of the labellum is easily accessible to insects with short probosces, and the flowers of Helleborine are therefore much frequented by wasps. I have selected *Vespa Austriaca* for illustration, as I have often observed wasps of that species on the flowers. On alighting the insect holds on with its legs to the embossed parts of the lip and proceeds to lick up the honey filling the cavity, beginning at the bottom and working up to the top. During the latter part of the operation its forehead must inevitably come into contact with the viscid projecting rostellum, which at once adheres to it (see fig. 268 [5]). In withdrawing from the flower, when the feast is over, the wasp draws the two pollen-masses attached to the viscid rostellum out of the anther-loculi, and flies away into the open air adorned with this curious head-dress (fig. 268 [6]). Not satisfied with the meal afforded by a single flower, it straightway seeks another and behaves here in the same manner as it did on the first occasion. During the time of flight from one flower to another the pollinia, sticking to the wasp's forehead, undergo a gradual tilting forward, the sticky gland remaining fixed at the same spot, but the pollinia becoming depressed; as a consequence of this change in their position, the pollinia are not shoved into the anther of the next flower the wasp visits, but are pressed against the quadrangular stigma (see fig. 268 [7]). This depression of the pollinia is much better marked in many other common Orchids, however.

In all essential respects the process above described is common to the majority of Orchids where the labellum has a downward inclination and there is only a single anther; but great variety prevails in respect of accessory details, as indeed is to be expected, when we consider the wide divergencies existing in the forms of the flowers and of their insect-visitors. A brief reference to two of the most striking modifications is all we can give here. The greatest variation is exhibited, as we said before, by the labellum and the rostellum. In some genera—in the Twayblade (*Listera*), for example—the part of the lip which contains the honey is not bowl-shaped, but in the form of a long, narrow furrow, and the secretion is licked up by small beetles. In other instances the back of the lip is produced into a spur lined with cells full of sweet juice, to which insects obtain access by piercing the walls of the cells. The genus *Orchis* affords an example of this. Honey of a sort peculiarly attractive to butterflies is secreted in the tubular spur in other cases, such as *Gymnadenia* and *Habenaria* (see fig. 258 [9], p. 227).

Two separate particles of viscid matter are often produced on the rostellum, each being in connection with one only of the pollen-masses (e.g. *Habenaria* *chlorantha,* the Large Butterfly Orchis). Insects then frequently only draw one of the pollen-masses out of the anther, instead of both, as they leave the flower. In species of the Twayblade genus (*Listera*) the rostellum is scale-like and arches over the stigmatic surface. At the commencement of the flowering period it is not connected with the pollinia, but the moment it is touched it exudes a drop of viscid fluid which sticks, on the one hand, to the body touching

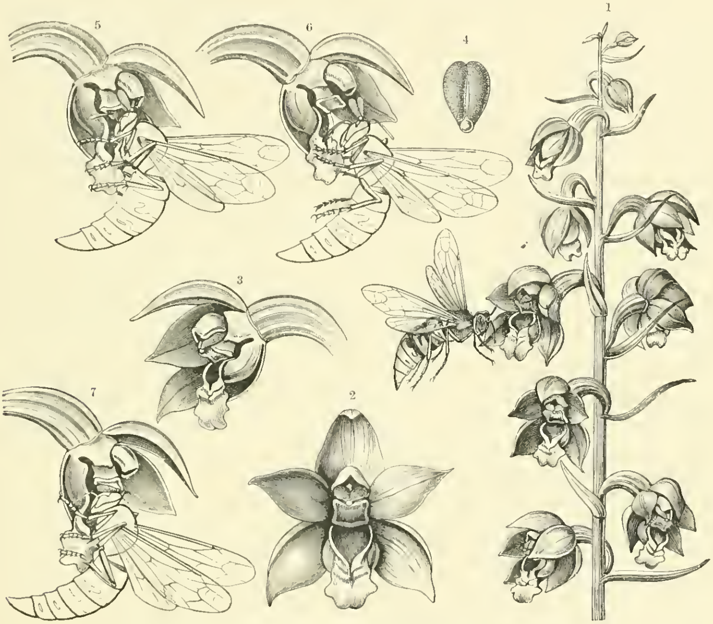


Fig. 268.—Withdrawal and deposition of pollinia in the flowers of an Orchid

Flowering spike of the Broad-leaved Helleborine (*Epipactis latifolia*) upon which a wasp (*Vespa Austriaca*) is alighting. [2] A flower of the same seen from the front. [3] Side view of the same flower with the half of the perianth towards the observer cut away. [4] The two pollinia joined by the sticky rostellum. [5] The same flower being visited by a wasp, which is licking honey and at the same time detaching with its forehead the tip of the rostellum together with the pair of pollinia. [6] The wasp leaving the flower with the pollinia cemented to its head; the pollinia are erect. [7] The wasp visiting another flower and pressing its forehead with the pollinia (which in the meantime have bent down) against the stigma. [1] nat. size; the other figures × 2.

it, and, on the other, to the pollinia surmounting the rostellum, and, hardening almost instantaneously, cements them together. The flowers are visited by small Hymenoptera belonging to the genera *Cryptus*, *Ichneumon*, and *Tryphon*, and still more frequently by little beetles of the genus *Grammoptera*. When an insect of any one of these genera lands on the labellum and proceeds to lick the honey-secreting furrow from the bottom to the top, it finds itself, towards the conclusion of its meal, in contact with the projecting edge of the rostellum. In a moment the pollen-masses are cemented to the forehead of the insect in the manner described, and are subsequently carried away upon a visit to another flower.

Strange to relate, the viscid masses sometimes adhere to the eyes of insects, although there can be no doubt that their power of vision is thereby curtailed. This occurs, in particular, in those Orchids where the anther-loculi and pollinia diverge from one another towards their bases and are connected with two separate viscid masses pertaining to the rostellum. In the flowers of *Habenaria montana* the pollinia are inclined to one another at an angle of 70° and form a kind of yoke under which it is necessary for butterflies to insert their heads if they want to suck the honey from the long spur. Thus the viscid discs, and, through their intervention, the pollinia are certain to attach themselves to either side of the intruder's head, and the eyes are frequently the spots where the adhesion happens to be effected. The genus *Habenaria* is also of interest inasmuch as it illustrates the fact that the particular minor variations in floral structure which are used to differentiate species always possess some special significance in relation to the visits of insects. The *Habenaria Hookeri* of the New World differs from the *Habenaria montana* of the Old World in having in the middle of the stigma a projecting lobe, the presence of which results in the formation of two entrances to the spur containing the honey. A butterfly visiting the flower only inserts its proboscis into one of the two passages, and therefore comes into contact with only one of the viscid discs and carries away but a single pollinium. Yet another arrangement is found in *Habenaria bifolia*, the Lesser Butterfly Orchis, which is widely distributed in Europe and Asia. In this species the pollinia lie nearly parallel and above the entrance, and they usually adhere simultaneously to one eye of the Sphingidæ which visit them (see fig. 258^{11}, p. 227), or to the base of the proboscis in the case of nocturnal Lepidoptera (Noctuæ of the genera *Agrotis*, *Hadena*, and *Plusia*). In the various species of *Gymnadenia* the pollinia adhere to the sides of the probosces of the small Noctuæ which suck their honey, whilst in the Musk Orchis (*Herminium Monorchis*) they become attached to the front feet of such little Hymenoptera and beetles as come to lick their sweet store. A long series of contrivances showing a wonderful correlation between the forms of flowers and those of flower-seeking insects might be added to these examples.

At the time when insects visit the flowers, the Orchids hitherto referred to, all of which have erect inflorescences, have their labella turned towards the ground owing to the stalk-like inferior ovaries being twisted (*cf.* Plate XIII.). Only quite a few Orchids, on the other hand, retain the parts of the flower in the same positions, after the bud is open and ready for insects, as were occupied by them in the bud. *Epipogium aphyllum*, a remarkable plant, which has been already referred to in respect of its peculiar mode of life (see vol. i. p. 111), may be taken as a type of this group. As shown in fig. 257 [10], p. 226 of the present volume, five of the perianth-segments of *Epipogium aphyllum* are long and narrow and slightly incurved. These segments inclose a space in the same sense as the curved fingers of a hollow hand may be said to do so, and in the middle of the space the column presents itself in the shape of a slightly ascending platform for insects to alight on. Arching over it is the sixth leaf of the perianth, the labellum, which resembles a cowl or helmet and causes the whole flower to look somewhat like that of Monkshood. Honey is concealed in the interior of the cowl, and in order to reach it the humble-bees which frequent this Orchid are obliged to crawl up the landing-stage with their bodies in contact with it, that is to say, with the column bearing the stigma and anther. The separate parts of the flower here are in the reversed position as compared with ordinary Orchids, where the labellum is the lowest member. The column bears the anther at its lower extremity, then comes the rostellum, which develops an extremely sticky disc, and still higher up, the steeply-sloping wall of the stigma (see fig. 257 [12]). The oval pollinia are attached to the viscid disc of the rostellum by long ductile filaments or pedicels (see fig. 257 [13]), and are covered over by a membranous hood, the anther-case. When an individual of the species of humble-bee named *Bombus lucorum*, a frequenter of shady woods, alights on the column of a flower of *Epipogium aphyllum* and proceeds to crawl from the lower edge of that structure towards the honey concealed in the galeate labellum, it does not at once come into direct contact with the pollinia, they being covered by the hood-like anther-case, but the viscid disc of the rostellum immediately adheres to the under part of the insect's body. Afterwards, when the bee leaves the flower, the anther-cap is thrown back and the two pollen-masses attached to the viscid disc are drawn out of their niches and carried away (fig. 257 [13]). The manner of their transference to other flowers will be discussed in the next chapter.

In many respects similar to these Orchid-mechanisms for promoting a transfer of the pollen are those prevailing in the flowers of Asclepiadaceæ, where the pollen masses are fastened by special organs of attachment to the feet of insects. Here again the pollen is in the form of pollinia connected together in pairs, and one cannot look at them without being reminded of the analogous structure in Orchids (see fig. 269 [4]). On nearer inspection, however, important differences are discovered to exist. In the first place, the little knob ("corpusculum") connecting the two pollinia is not soft and viscid as in Orchids, but is a hard, dry implement with two arms capable of holding any small delicate object by gripping it like a clip; secondly, the pollinia are not clavate or of pasty consistency, but are in the form of shining horny leaflets; and thirdly, the two pollinia which are attached to the clip-like body by ligulate strands belong to two adjacent stamens instead of to a single one. A transverse section through the flower of *Asclepias Cornuti* (see fig. 269^{3}) shows in the centre a five-sided column; adnate to each of its sides is a tumid bilocular anther with membranous wings running down its lateral margins. The wings are not appressed to the column, but are reflexed, and stand out in pairs, with the free margins of the two wings in each pair converging towards one another. This produces the same effect as if the anthers coating the central column were slit through longitudinally in front of every corner of the pentagon. Owing to the fact that the swollen part of each anther bears a curious excavated structure, it comes about that the pollen-producing portions of the anthers are nowhere visible externally save the membranous wings or the five apparent slits, as is shown in figs. 269^{1} and 269^{2}). The hollow staminal appendages are full of honey, and each is embellished by a central process shaped like a horn. At the back of every one of the five slits is a little clip-like organ from which proceed ligulate strands connecting it with the pollinia in the adjacent loculi of two different anthers (loculi have vertical shading in fig. 269^{3}), the pollen-mass in the left loculus of the anther to the right of the slit being thus associated with the pollen-mass in the right loculus of the anther to the left of the slit. The abundant honey in the staminal appendages emits a scent perceptible from afar, and attracts numberless insects to the flowers. The honey, being stored in a very superficial position, is accessible to insects with short probosces, and, therefore, the chief visitors besides hive- and humble-bees are wasps and Fossores, and these bright-coloured glossy insects—especially the splendid Scolias (*Scolia hæmorrhoidalis, S. quadripunctata, S. bicincta*)—are a beautiful sight as they hover about the blossoms. During the time when the honey is most abundant the flowers are either nodding or pendent, and they offer no convenient place for the insects to alight upon, or from which

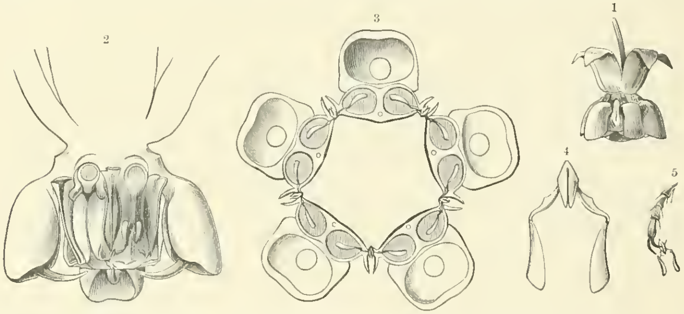


Fig. 269.—Clip-mechanism for fastening the pollinia of *Asclepias Cornuti* to the feet of insects.

[1] Flower of *Asclepias Cornuti* seen from the side. [2] The same magnified and with two staminal appendages and the front wall of an anther cut away. [3] Transverse section through the same flower. [4] Corpusculum (the clip) with two pollinia. [5] Foot of an insect with pollinia fastened to it by the clip. [1] nat. size; the other figures × 2-5.

they can comfortably suck the honey. All parts of the flower are smooth and slippery, and the only way in which an insect can support its weight is by inserting its claws in the slits between the anthers. In endeavouring to take firm hold, the insect draws its claw from one end of the slit to the other, and so becomes attached to the clip-like organ at the back. When the insect's foot is withdrawn the two pollinia adherent to the clip are dragged out of their niches. One of the claws on that foot is then seen to be wedged between the arms of the clip, whilst the two pollinia are suspended from it (see fig. 269 ^{5}).

The subsequent history of the pollinia does not strictly belong to the subject of this chapter, but it will be convenient to follow them to their destination. The pollen-masses must be conveyed to stigmas of other flowers. The question is, where are these stigmas to be found? The pentagonal central column, surrounded by the five anthers, contains the ovary in its interior. The approaches to this organ lie through the so-called stigmatic chambers, which are situated close beneath the truncate end of the column, and open outwards. The chambers are concealed in the slits, just as were the clip-like organs, and insects occasionally come across them as they move their claws about in the recesses. If the foot inserted by an insect has pollinia already attached to it, they are thus introduced into the slit in a new flower, and as the insect feels about for firm support it thrusts the pollinia into the stigmatic chamber. When the foot is subsequently withdrawn, the ligatures attaching the pollinia to the little clip are broken, and the pollinia are left in the chamber, whilst the actual clip maintains its grip of the claw. A second organ of the kind with its pollinia may become attached to the insect's foot on this occasion, and the process may indeed be repeated a number of times. Insects caught after visiting flowers of *Asclepias Cornuti* have often been found to have from five to eight of these clips fastened to a single foot.

Other members of the Asclepiadaceæ have essentially the same mechanism, though differences in detail of course occur. Very interesting is the result of cultivating the asclepiad *Araujia albens* (*Physianthus albens* of gardeners) in regions in which it is not indigenous. This plant is a climber from S. Brazil and Buenos Ayres, and being an ornamental plant is cultivated in gardens in various parts of the world. In its own country it is visited normally by humble-bees, and the curious phenomenon to be described has not been reported as occurring there. But in other localities its sweet-smelling, tubular flowers are visited by hosts of moths, which are apparently unacquainted with the mechanism of the pollen-masses, &c., and get trapped by their probosces in the slit-like notches, which are present between the anther-wings. These wings are rigid, and the slit narrows upwards, and moths visiting the flowers for honey get their probosces jammed in the slits. The result of their struggles to free themselves is only to fix their probosces the tighter in the narrow end of the slit, and the moths die a lingering death with their heads concealed in the tubes of the corollas, and their abdomens projecting. Reliable testimony of this moth-catching propensity of *Araujia albens* is forthcoming from Massachusetts (Providence), from Italy (Cagliari), and from the Orange Free State. The victims include *Plusia precationis, P. Gamma,* and *P. ehrysitis, Picris Brassicæ, Deilaphila Euphorbiæ,* &c.

This clamping of pollinia to the feet of insects is quite unique amongst phenomena of the kind observed in the whole realm of plants, and it would be scarcely surprising if people who have not seen the operation with their own eyes were to look upon it as the offspring of a botanist's imagination. There are, however, in the same category, four other cases of behaviour equally calculated to excite astonishment in the observer, and these are all the more remarkable from the fact that in them the transference of pollen to the bodies of insects is effected by means of special movements of different parts of the flower. The insects do not dust off the pollen by coming into immediate contact with it, but their entrance into a flower causes certain changes in the position of the various parts resulting in the pollen being sprinkled, thrown, or rubbed upon particular parts of the intruder's body.

I do not like comparing these contrivances in plants to the devices of human ingenuity; but the analogy existing between the various kinds of mechanism which effect the transfer of pollen and machines, invented by man, is so close that it would be affectation to refuse to take advantage of the fact that the action of these contrivances in plants can be rendered much more easily intelligible by describing them in terms which plainly indicate their resemblance to simple appliances in use in every household. We shall, therefore, differentiate the various kinds of mechanism for loading insects with pollen, which still remain to be discussed, into those provided with piston-apparatus; hammers, or percussive apparatus; springs, or explosive apparatus; and sprinklers.

To begin with, let us take the *piston-apparatus* in Papilionaceæ. In very many though not all Papilionaceæ the two lateral petals, called *alæ* or wings, converge towards their upper margins, along which they are in contact, so that they form a convex saddle arching over the keel. This arrangement may be seen, for instance, in *Coronilla*, the Horse-shoe Vetch (*Hippocrepis*), the Lupine (*Lupinus*), the Rest-harrow (*Ononis*), *Anthyllis*, and in the Bird's-foot Trefoil (*Lotus corniculatus*; see figs. 270^{1} and 270^{2}), the last being the species here selected for illustration. The wings are connected with the keel in a peculiar manner. Near the base of each wing is a projecting fold which exactly fits into a socket in the corresponding half of the keel (see figs. 270^{3} and 270^{4}). Thus wings and keel are locked together, and every pressure upon the pair of alæ is transmitted tc the keel. Consequently when a hive- or humble-bee sets itself astride on the saddle-ridge formed by the wings, not only is the latter pressed down, but also the keel; and this movement is accompanied, to the astonishment of the observer, by the extrusion of a pasty vermicular mass of pollen through a small opening at the conical apex of the keel, and by the simultaneous adhesion of the pollen to the insect's belly, or sometimes to its legs. The process of expulsion is shown in figs. $270^{5,6,7,}$ where a number of stamens lying close together are seen to be thickened into clubs at the part just below the anthers. This bundle of stamens shuts off at the free end of the keel a hollow cone which is open at the apex only, and the action of the stamens within the cavity is just the same as that of the piston inside a pump. When the keel is depressed by a force acting in the direction of the arrow (fig. 270[6]), the stamens, being fixed, are forced further into the conical cavity and push part of the pollen stored in it through the small orifice at the top. When the pressure ceases the keel returns to its former position. It has been ascertained by careful observations that the process of pumping pollen from a particular flower may be repeated eight times, provided that the keel is not pressed down too low, and that when the keel is depressed beyond a certain extent the end of the style also protrudes through the opening (see fig. 270[7]) and comes into contact with the abdomen of the bee which is visiting the flower at the time.

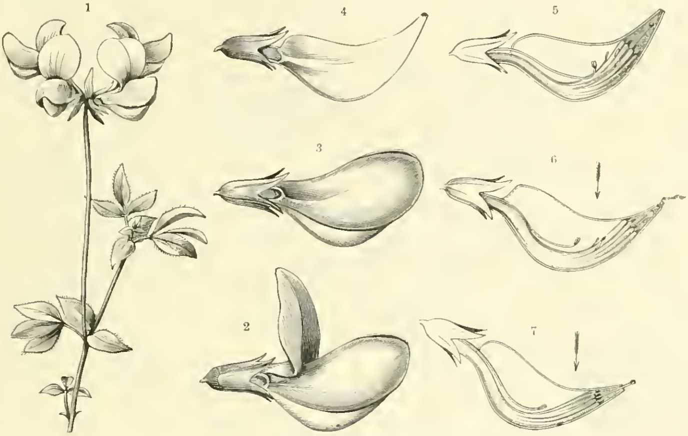


Fig. 270.—Apparatus for pumping pollen on to the bodies of insects.

[1] *Lotus corniculatus.* [2] Single flower of the same × 2. [3] The same flower with the standard removed. [4] The same flower with the standard and the wings removed so as to expose the keel. [5] One component leaf of the keel removed; in the interior of the keel are seen the stamens, the longer ones clavately thickened towards their free extremities; the conical cavity above the anthers (which are empty) is full of pollen, and the style and stigma are embedded in the mass of pollen. [6] Depression of the keel in the direction indicated by the arrow, in consequence of which pollen is pumped out of the orifice of the conical cavity by the bundle of clavate filaments. [7] The keel still further depressed in the direction of the arrow so that the stigma is extruded through the orifice at the apex of the hollow cone.

This kind of pump-apparatus appears to be confined to papilionaceous flowers. On the other hand, the mechanism to be described next, which does its work by means of impact, occurs in flowers belonging to the most diverse families. In every case of the kind the movement of the filaments, which results in the transfer of pollen to the body of an insect, resembles the striking of the hammer on a bell, although the cause of the movement is not the same in the different flowers. Sometimes a two-armed lever is set in motion; sometimes there is a sudden recoil of the stamens due to their liberation, as it were, from a vice, and in a third class of cases the filaments are irritable and on the slightest touch undergo a change of position analogous to the closing up of the leaves of the Sensitive Plant (*Mimosa*; see vol. i. p. 537) when subjected to a like stimulus.

The best known examples of the hammer form of mechanism occur in the genus *Salvia*. In no species of that large genus is it developed to greater perfection than in *Salvia glutinosa*, which we therefore select for illustration. The flowers of this Labiate are set laterally on the stem, and the under-lip serves as landing-stage for the humble-bees to alight on (see fig. 271). If a bee, after alighting, is to obtain the honey which is hidden in the back part of the flower near the ovary, it must advance from the under-lip into the gaping jaws of the flower. It is there that the curious mechanism is set ready. On either side of the entrance is a stamen (see fig. 271^{3}) composed of a short, erect, firm, and immovable filament, and an anther borne at the extremity of a much elongated and slightly curved connective which rocks at the top of the filament. The connective is articulated to the filament in such a manner as only to be able to swing in the direction indicated in figs. 271^{4} and 271^{5}. The part of the stamen which is liable to be set rocking is a curved lever consisting of two arms of unequal length. The upper arm is the longer and terminates in the anther, whilst the under and shorter arm is somewhat thickened and spatulate at its free extremity. When a humble-bee pushes the lower arm in the direction of the arrow (fig. 271^{4}) the upper arm drops (fig. 271^{5}).

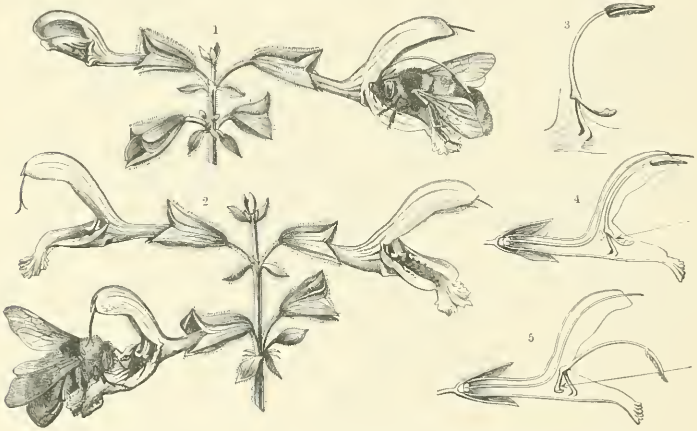


Fig. 271.—Transference of pollen to the bodies of insects by means of mechanism of the percussive type.

^{1} Part of an inflorescence of *Salvia glutinosa*; the right-hand flower is being visited by a humble-bee, and the pollen-covered anther is in the act of striking the insect's back. ^{2} Another part of the same inflorescence with three open flowers in different stages of development: the lower flower on the left-hand side is being visited by a humble-bee which carries on its back pollen from a younger flower and is rubbing it off on to the deflexed stigma. ^{3} A stamen of *Salvia glutinosa* with rocking connective. ^{4} Longitudinal section through a flower of the same plant. The arrow indicates the direction in which humble-bees advance towards the interior of the flower. ^{5} Same section; the lower arm of the connective-lever is pushed backward, and in consequence the pollen-covered anther at the end of the other arm of the lever is deflexed.

As the two stamens are close together and the lower arms of the connective practically touch one another, the upper arms fall simultaneously, and anyone observing the phenomenon from the side might think there were only a single rocking anther in the flower. Thus, when a humble-bee, making its way from the landing-stage of the under-lip to the floral receptacle, comes against the pair of short lever-arms barring the entrance, the anthers drop simultaneously upon its back and cover it with pollen (271^1). We shall show in a subsequent section that bees laden in this manner rub the pollen off on to the deflexed stigmas of the flowers they subsequently visit (271^2). The hammer-apparatus in the flowers of *Salvia officinalis,* which grows broadcast on the shores of the Mediterranean, only differs from the above in that a little pollen is developed in addition at the end of the lower arm of the lever, and is brushed off on to the head of the insect. The rocking part of the stamen in every species of *Salvia* must be looked upon as an anther with a specially modified connective. The connective is transformed into a long curved lever bearing an anther-lobe at each end. In *Salvia glutinosa* only the lobe at the upper end is polliniferous, whilst at the lower extremity there is a complete absence of pollen. In *Salvia officinalis,* on the other hand, a little pollen develops, as we have seen, in the smaller lobe at the end of the shorter arm also. In the numerous species of which *Salvia pratensis* is a type the filaments are extremely short, and the lower arm of the lever in each case is metamorphosed into a quadrangular flap or valve. The flaps of the two opposite stamens are joined so intimately together that they close the mouth of the flower like a trap-door. Each valve, however, has a little notch in the side adjoining the other, and the two notches coincide so as to form an orifice in the middle of the trap-door. Insects insert their probosces through this hole, and in so doing push the trap-door backwards and upwards. The valves of the trap-door being also the short arms of the lever-apparatus, their ascent is accompanied by the descent of the long arms, each of which bears an anther-lobe full of pollen at its extremity, and in this manner the upper surface of the insect's body is covered with pollen as it sucks the honey.

In the Lopezias indigenous to Mexico, the effect of the striking of insects by the anthers is to load, not the upper, but the under surfaces of their bodies with pollen. These plants (*Lopezia coronata, L. miniata, L. racemosa*) are remarkable for having only a single anther-bearing stamen in each flower. The stamen is wedged in a sterile, petal-like staminode inserted immediately below it; this staminode has its free end fashioned into the shape of a spoon. This spoon-shaped extremity affords the most convenient alighting-place, and the moment an insect settles upon it the staminode suddenly flaps down, whilst at the same instant the stamen concealed within it (being previously in a state of tension) springs up, striking the under surface of the insect's body and covering it with pollen.

The flowers of the Barberry (*Berberis*) have irritable filaments which cause the anthers to strike against insects. There are six stamens arranged in two whorls in each flower; they slope obliquely outwards, and are concealed in the concave petals which are inserted behind them. Honey is produced in abundance from saffron-coloured swellings on the petals, and is to be found in the interior of the flower sticking to those sides of the filaments which face the ovary. Both hive-bees and humble-bees covet this honey and fasten on to the pendent racemes to obtain it. Often, in the very act of laying hold of a flower, an insect inserts its forelegs into it and touches the stamens; but even if this does not happen, the bases of the stamens are sure to be touched when the insect introduces its proboscis to suck the honey. The slightest touch administered to the lower third of a stamen's length acts as a stimulus, and results in an alteration in the tension of the tissues, and in a sudden backward movement or up-springing of the stamen. The anther is thus caused to strike upwards against the insect, covering its head with pollen, whilst the proboscis and forelegs are also besmeared, though to a less degree.

The transference of pollen to the bodies of insects takes place in the *Opuntia* in the same manner as in the Barberry. The comparatively large flowers of *Opuntia nana*, which grows in Dalmatia and near Sion in the Rhone Valley, &c., open at nine o'clock in the morning when the sky is clear. The fleshy four-lobed stigma may then be seen crowning the thick conical style and forming obviously the most convenient place for insects to alight on. The style rises out of a pit which contains a copious supply of honey, and is surrounded by a large number of erect stamens of different lengths. The dehiscent anthers are charged with pollen of a crumbly consistency; the filaments have the lowest quarter of their length coloured pale yellow and the upper part bright gold. If the golden region of the filament is touched, it curves inwards, forming a semicircular and slightly twisted bow, surmounting the honey-receptacle out of which the style rises. When a bee visits the flower, it settles first on the large stigma, which projects above the anthers, and then tries to clamber down to the honey. During this process contact with the irritable portion of the filaments is inevitable, and the moment it occurs the stamens that are touched bend over the bee and load it with their pollen which is easily detached from the anthers. It is amusing to watch this phenomenon and observe how quickly one after another the filaments bend over the insect, and administer their blows as it crawls down. The bee is not much alarmed by the inflection of the filaments, or by the taps it receives, but suffers itself to be loaded with pollen without making any fuss. It is able to brush it off subsequently and collect it in the "honey-baskets" borne on the tibiæ of its hind-legs. As the inflection of the stamens lasts at least until the insect leaves the flower, a further supply of pollen is sure to be rubbed off when the bee begins to retreat. Usually, when bees leave *Opuntia* flowers, they are dusted all over with the yellow pollen.

Part of the pollen, in the case where the anthers belong to a mechanism of the percussive type, is appressed and affixed to the insect's body, whilst part is brushed off owing to the movements of the creature when it takes its departure from the flower. In this respect the apparatus differs from contrivances of the *explosive* variety, which are adapted to besprinkle or bespatter insects with pollen. The explosion is due to a sudden up-springing of some organ, which may be the style, the filaments or, as in a few Orchids, the anthers and rostellum. The number of these contrivances is very large, and I must therefore confine myself to an account of the most curious forms, beginning with the case of *Crucianella stylosa*, which grows native in Northern Persia, and is represented in figs. 272 and 274[1]. This plant belongs to the Stellatæ group of Rubiaceæ. Its rose-coloured flowers are conglomerated in terminal heads (274[1]), and scent the air with honey to a considerable distance. If one side of the corolla be removed, the first peculiarities that strike the observer are that the long slender style is twisted into a spiral, and that the thick stigma at the top of it is wedged between the anthers (see fig. 272[1]). The moment the anthers open the pollen pours out of the loculi and rests upon the papillose surface of the stigma (fig. 272[2]). Soon afterwards the style elongates and its coils relax somewhat, the result being that the stigma, with its coating of pollen, is carried up above the now empty anthers until it comes against the dome-shaped top of the closed corolla where its further ascent is stopped. At this stage of development (fig. 272[3]) the style is in a condition of such extreme tension that the instant the limb of the corolla opens it springs up, scattering a cloud of pollen from the surface of the stigma (fig. 272[4]). In the absence of insects this ejection of

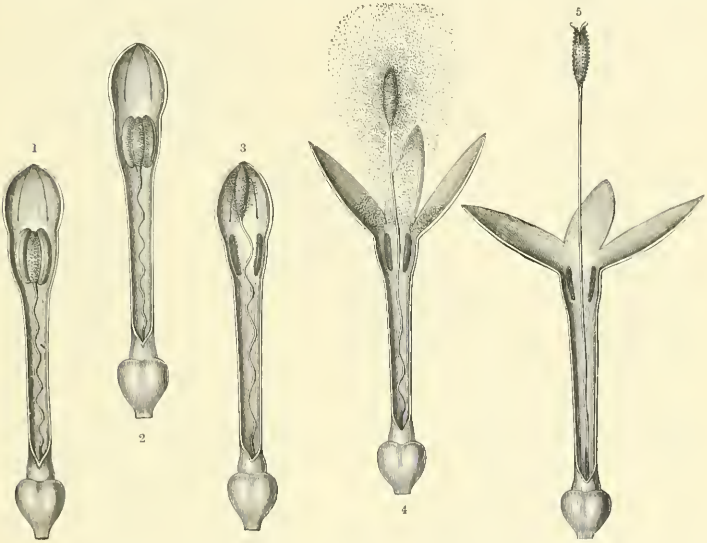


Fig. 272.—Explosive apparatus for the transfer of pollen to the bodies of insects

[1] Longitudinal section through the unopened flower of *Crucianella stylosa*; the papillose stigma wedged between the closed anthers. [2] The same after the dehiscence of the anthers; the pollen deposited on the papillose surface of the stigma. [3] The stigma covered with pollen has been carried up owing to the elongation of the style until it rests under the dome of the closed flower. [4] The corolla has burst open, and the style, springing up suddenly in consequence, is discharging the pollen from the surface of the stigma. [5] The style projects far beyond the corolla and bears the open two-lipped stigma which is now first mature and ready to be pollinated. All the figures × 4.

pollen takes place spontaneously; but a sudden opening of the corolla-limb is caused if a small bee or fly chances to touch the top of a closed flower on its way to visit an open one, and the insect is then dusted with pollen from below as is shown in fig. 274 [1]. The subsequent events occurring in these flowers will be described later on, and an explanation of fig. 272 [5] will then be given.

The species of the genus *Schizanthus*, indigenous to Chili and Peru, one of which—*Schizanthus pinnatus*—is cultivated in our gardens as an ornamental plant, have long been known to possess mechanism for the explosive distribution of pollen. The most conspicuous object in the open flower of any of these plants is a single up-turned speckled lobe, whose function it is to attract insects. Beneath it are two smaller incised lobes which form a sort of keel, affording a convenient place for insects to alight on. Fixed firmly in the furrow of this keel are two stamens, which are released the moment an insect settles on the keel and introduces its proboscis underneath the vexillary petal above described. The stamens then spring up, and the pollen is scattered out of the anthers.

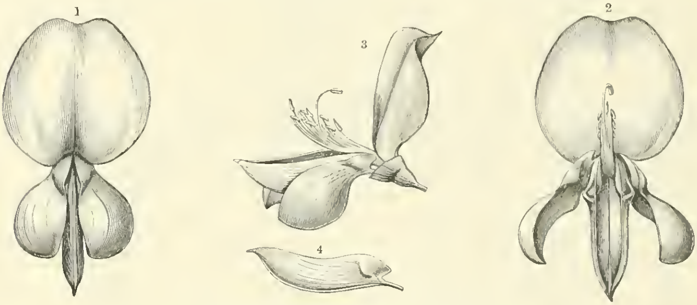


Fig. 273.—Explosive apparatus in a papilionaceous flower.

[1] Flower of *Spartium scoparium* (*Sarothamnus scoparius*) seen from the front, the keel closed. [2] Same flower with the keel open; the stamens previously concealed there together with the style have sprung up. [3] Side view of the same flower after the opening of the keel and springing up of the stamens. [4] One of the two component petals of the keel seen from within.

The occurrence of a similar up-throwing of pollen in the flowers of the Yellow Corydalis and a few other species of the same genus (*Corydalis lutea*, *C. ochroleuca*, *C. acaulis*) has been already noted (p. 228) in the account given of the stirrup-shaped lobes on the sides of those flowers. We have only to add that the articulation of the projecting left-hand petal to the two contiguous median petals forming the saddle ceases the moment an insect sprawls upon the saddle and inserts its proboscis underneath the spurred petal. This disconnection has the immediate effect of causing the saddle to drop and the stamens hitherto concealed in the cavity to spring up. The meal-like pollen of *Corydalis* being liberated early, is by that time lying loose upon the anthers, and is ejected upon the under surface of the insect when the stamens are thus suddenly released (cf. figs. 257 [3] and 257 [4], p. 226).

The phenomenon of an upward discharge of pollen is also well exhibited in the Melastomaceæ and in many Papilionaceæ of the genera *Astragalus, Indigofera, Medicago,* and *Phaca,* as also in *Genista, Retama, Sarothamnus, Spartium,* and *Ulex.* We will select *Spartium scoparium,* a plant belonging to the Mediterranean Flora (figured in vol. i. p. 331), as a representative of this group. Figs. 273^1 and 273^2 show the front views of a flower of *Spartium scoparium,* and one recognizes at once the large upturned standard, the two lateral petals and underneath them the keel composed of a pair of contiguous petals. Near the base of each keel-petal is observed a swelling and a depression (fig. 273^4), which correspond with portions of the structure of the two wings, so that the latter pair of petals locks with the keel, and every pressure upon the wings from above affects the keel also. A blunt tooth may also be seen near the base of each of the wings (see fig. 273^3). When the flower is closed the teeth are hidden under the standard; in the open flower they are pressed against the standard, and so keep the wings, and indirectly the keel, in a horizontal position.

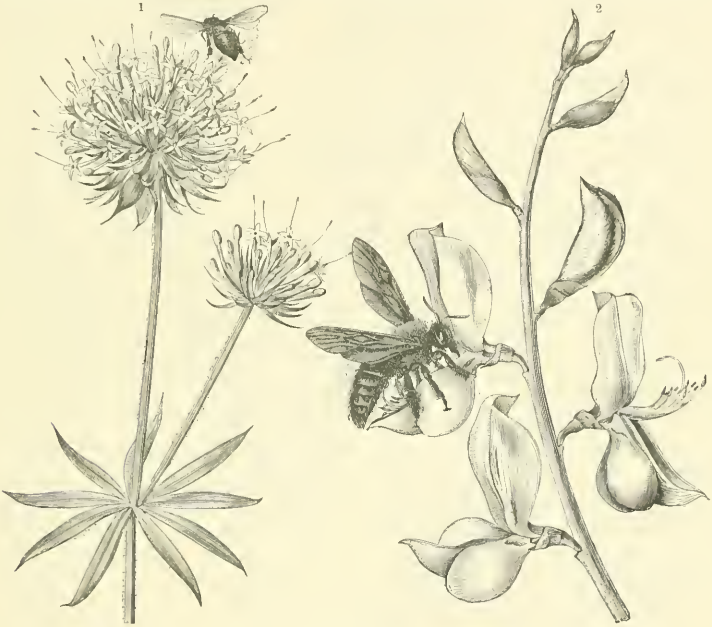


Fig. 274.—Transference of pollen to the bodies of insects by means of explosive apparatus.

^{1} *Crucianella stylosa*; the pollen is being discharged from the flowers on to the belly of a hymenopterous insect. ^{2} *Spartium scoparium*; in the lowest flower the keel is still closed and stretched out horizontally; in the flower next above, the keel is depressed and the stamens have sprung up; the third flower is being visited by a Carpenter Bee (*Xylocopa violacea*), and is ejecting its pollen on to the under surface of the insect's body.

In the keel are concealed a style and ten stamens, all in a state of tension like watch-springs. The anthers liberate their pollen very early, and it accumulates in the front part of the keel. When the pulvinate wings, and through them the keel, undergo pressure from above, the blunt teeth which fasten the wings and keel together slip down, and both wings and keel fall with a sudden jerk, whilst the stamens and style lying at the bottom of the keel spring up, throwing the mealy mass of pollen into the air. In nature the object to which the pressure on the wings is due is usually a largish insect, and the result is of course just the same, so that the under surface of the creature's abdomen receives the discharged pollen (fig. 274 [2]).

The pollen in these flowers being of floury or powdery consistency, a great cloud of dust is emitted whenever the explosive mechanism is brought into play. The same effect is produced as if the flowers exploded, and several of the plants in question—as, for instance, the various species of the genus *Schizanthus*—are called by gardeners "plants with explosive flowers". Apparatus for ejecting the whole of an anther's pollen at once in a single coherent mass are of much rarer occurrence. The flowers of a Brazilian shrub named *Posoqueria fragrans*, belonging to the order of Rubiaceæ, and those of a few tropical Orchids are especially remarkable in this respect. The blossom of *Posoqueria* reminds one in many ways of that of the Honeysuckle, exhibiting like the latter a corolla composed of a long horizontal tube and five short limb-segments which are somewhat reflexed when the flower opens. The opening takes place in the evening; the corolla is white, secretes honey at the bottom, and emits at dusk and during the night a pervading scent—all characteristics of a nature to indicate that the flowers are adapted to the visits of Sphingidæ. The abundant honey at the base of the tube can only be reached by the tongues of Sphingidæ; and only these insects, *e.g. Sphinx rustica,* whose proboscis is 15 mm. long, have been seen to visit the flower.

The five anthers are united into an oval knob directed obliquely downwards and containing the loosely-coherent pollen which escaped from the anthers before the expansion of the flower. The filament of the lowest stamen possesses a very considerable elastic tension acting upwards; those of the upper and lateral stamens have a similar tension outwards. The insect's proboscis has only one available point at which to enter the flower, and when in doing so it touches one of the upper stamens at a certain spot the tension of the stamens is released. The lowest stamen springs up with such violence that it hurls the loosely-coherent pollen against the insect's proboscis at an angle of 50° with the tube of the corolla, and with an initial velocity of about 3 mm. per second; at the same time it closes the entrance to the tube. The upper and lateral stamens spring at the same time to the sides, the empty anthers of an upper and a lateral stamen remaining coherent on either side. About twelve hours afterwards the lowest stamen extends itself again and leaves the entrance to the flower open once more. If a hawk-moth, after exploding a flower in the first stage, comes to one in the stage under consideration, it is repaid for its startling reception in the former case by a rich supply of honey; and in thrusting its pollen-dusted proboscis down to the base of the flower it brings it in contact with the stigma, which stands in the middle of the tube.

The most noteworthy cases of Orchids furnished with expulsive mechanism are those of the genera *Catasetum* and *Dendrobium*. *Catasetum* will need a somewhat detailed account, for the reason that in this genus the process of expulsion ensues upon an external stimulus which does not act upon the mechanism in question direct, but is transmitted through a special organ. The column in the flower of *Catasetum* (see figs 275^{1} and 275^{2}), as in many other Orchids, rises

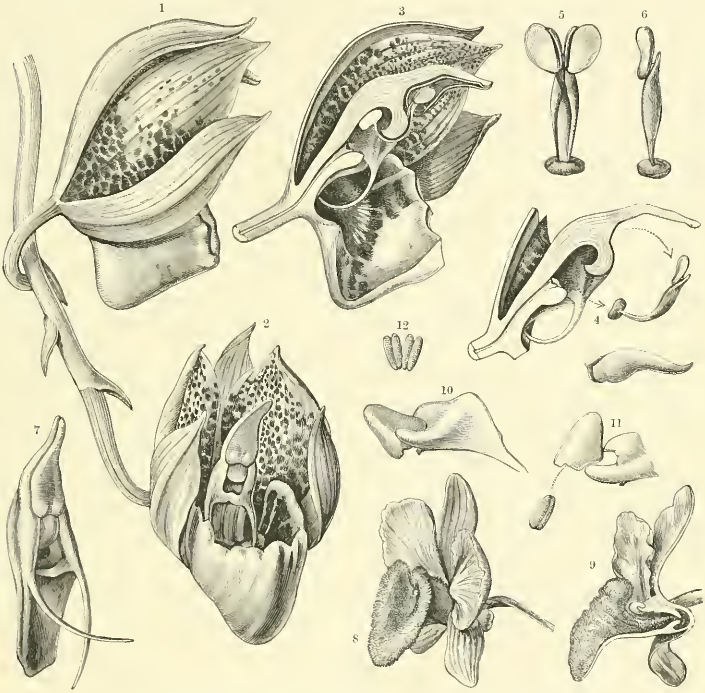


Fig. 275.—Expulsive apparatus in Orchid-flowers: flower of *Catasetum tridentatum*.

^{1} Side view. ^{2} Front view. ^{3} Longitudinal section through the same; the band connecting the pollen-masses with the viscid disc is stretched like a bow over the protruding rostellum. ^{4} The pollen-masses and viscid disc are liberated and are being jerked away by the sudden straightening of the connecting-band; the anther-case which hitherto concealed the pollen-masses tumbles away at the same time (below). ^{5} Front view of pollen-masses, viscid disc, and the band connecting them; the margins of the band somewhat involute. ^{6} Side view of the same. ^{7} Column removed from the flower; towards the summit is the anther, below it the elastic connecting-band stretched like a bow; next the stigmatic chamber with its fleshy margins prolonged into two horn-like irritable processes. ^{8} Flower of *Dendrobium fimbriatum*. ^{9} The same in longitudinal section. ^{10} Side view of the hood-like anther at the end of the column. ^{11} The anther jerking back and ejecting the pollen-masses. ^{12} Pollen-masses of *Dendrobium fimbriatum*. ^{10}, ^{11}, ^{12} × 5; the rest natural size up over a hollow labellum. Near the apex of the column is the anther, and lower down the rostellum, whilst below the rostellum the column is deeply excavated. The edges of this pit are fleshy, and are prolonged into two curious processes resembling a pair of horns. These processes are curved and tapering, and are inclined obliquely forwards and downwards. In most species, including *Catasetum tridentatum* (here represented), the horns (or antennæ, as they are sometimes called) cross one another diagonally (see fig. 275^{7}). Each horn, originally a ribbon-like lobe, is rolled up lengthwise so as to form a tapering tube. The substance of both horns passes without any definite line of demarcation into the tissue of the rostellum above. Although this tissue has been examined with the greatest care, nothing special has been found in it to account for the extraordinary irritability which it exhibits. It has been ascertained by experiment that any pressure on the lower extremity of the horn acts as a stimulus, and that this stimulus is at once transmitted upwards through the cells of the tissue to the part of the rostellum which forms the viscid disc. The slightest touch applied to the tip of one of the horns is instantly followed by the rupture of the tissue which has hitherto retained the viscid disc in position, and by the consequent liberation of that portion of the rostellum. The viscid disc had, however, in its turn served to keep a curved elastic band which attaches the disc to the pollinia on the stretch, and in its proper position (fig. 275^{3}), so that when the disc is set free the band flies up and straightens itself up with a jerk. The viscid disc and the pollinia are torn from their recesses by the recoil of the band, and are carried with it in an ample curve away from the column, which till then has served as their common base (fig. 275^{4}). During its flight the viscid disc goes first, and it naturally, by sticking to some object in the way, brings the pollen-masses to a standstill. From the time of its being shot off, the band connecting the disc and the pollinia is quite straight (see figs. 275^{5} and 275^{6}).

The expulsive apparatus exhibited by most species of *Dendrobium* is altogether different. In the species selected for illustration—viz. *Dendrobium fimbriatum* (figs. 275^{8} and 275^{9})—the column is capped by an anther in shape like a bell. The anther is septate, and contains in its loculi pollen-masses, which since they are unconnected with any viscid disc, are therefore liable to fall out of the anther in certain positions of the latter. The anther is borne by a slender subulate filament, to the extremity of which it is articulated in such a manner that a gentle push is sufficient to set it rocking. When the flower first opens, and before it has yet been exposed to any contact, the bell-shaped anther rests mouth downwards on a notch at the top of the column, and is held in that position by two tooth-like processes to the right and left of the notch (see fig. 275^{10}). A push administered from the front displaces the anther and causes it to fly back, whilst the pollinia contained in it are simultaneously expelled (see fig. 275^{11}). The pollinia being unfurnished with viscid discs (fig. 275^{12}), it is not quite evident how the insects which supply the necessary stimulus on their visits to the flowers get loaded with the pollen. There is, however, every probability that the expulsion is followed by a transference of the pollen to the bodies of the insects. Unfortunately we do not know of any observations having been made of the visits of insects to plants of this species in the wild state. Such observations might enable us to come to a sure conclusion on the subject, but so far all our results have been derived from flowers reared in hot-houses.

Next to the expulsive variety of mechanism comes the *sprinkling* variety. Pollen transferred by this kind of apparatus is always of mealy or powdery consistency, and is shaken out of the loculi where it is produced. Three modifications of this apparatus may be distinguished, viz.:—the sugar-tongs modification; that in which the anthers dehisce by terminal pores; and that in which the anthers are united into cones. In contrivances of the first kind, the filaments are like the arms of a pair of sugar-tongs, and the anthers borne by them are, when in the dehiscent condition, in the form of spoon-shaped receptacles or recesses, with the concave sides facing one another. Pollen of mealy consistency would not stay in open, upright spoons of the kind were it not for a special contrivance. In order to picture the state of things it is best to think of the action of a pair of sugar-tongs in which the end of each arm is fashioned into a spoon. When the tongs are closed the concave surfaces of the spoons are brought together, and form a receptacle in which sugar can be retained in the form of little solid bits, and even in the form of fine powder if the parts of the tongs fit well. The moment the two arms of the tongs are separated the contents held by the spoons drop down, and if in the condition of powder they must inevitably bepowder any object that may happen to be underneath. Now, this is just what occurs in connection with the sprinkling apparatus in the flowers of a large number of Acanthaceæ, Rhinanthaceæ, and Orobanchaceæ. Beneath the protective covering of the floral envelopes—most commonly under the upper lip of a bilabiate corolla—are found the stamens arranged two and two, with the anthers of each pair closed together like the two valves of a leguminous pod. They are kept in this position by the stiff staminal filaments, and the margins of the valves fit one another so exactly that not a single pollen-cell from the mass of floury pollen contained between them can fall out unless the structure is subjected to some particular shock. In some cases each pair of opposite valves is furnished with matted hairs which join the upper edges together. The form is then like that of a mussel-shell, and only the free margins can open. The moment the valves separate in the least, whether they are joined together at one part or not, the pollen spills out in accordance with the law of gravity. The direction of its fall is often determined by delicate hairs fringing the margin of the anther, the object being to prevent waste. The separation of the valves is caused by insects—and in tropical regions probably by humming-birds as well—when they press into the jaws of the flowers in search of the honey stored in the back-ground. In doing so the proboscis (or beak) is either pushed right between the valves, or it strikes against certain special processes with which the valves are furnished, or else the tense filaments bearing the valves are forced asunder. The first is what occurs in *Bartsia alpina*. In the flowers of this plant the entrance is much narrowed, owing to the curving up of the limb of the underlip, and close behind the entrance are found the anther-valves, which are comparatively large, and are edged at the top with matted hairs. Before an insect can reach the honey on the floral receptacle it has to force apart the lower edges of these valves, thus letting the pollen fall out upon itself. In the flowers of the Yellow-Rattle and Toothwort (*Rhinanthus, Lathræa*), the entrance is still more exactly defined, and the insect cannot deviate a hair's-breadth from it without sustaining injury. The filaments bearing the valves, which in this case are posted in the middle of the entrance, are beset with rigid prickles liable to injure an insect's delicate proboscis, and the only safe path to the receptacle lies between the ciliated anther-valves, which part asunder on being pushed with any moderate force (see figs. 277 [4, 5, 6]). In *Clandestina, Trixago*, and several other Rhinanthaceæ, the filaments are not furnished with prickles, but each anther bears a little downwardly-directed process which is pushed on one side by an insect entering the flower. The corresponding anthers are parted by the displacement of the processes, and the floury pollen is sprinkled upon the head and back of the intruder. In flowers of the Lousewort genus,—*Pedicularis asplenifolia, P. rostrata*, and many species allied to them—the anthers are hidden under the arch of the upper lip, and it is impossible for insects to come into direct contact with them. The path of the insects here lies somewhat deeper between the filaments, which they force apart, causing thereby a corresponding change in the position of all the different parts of the flower. In consequence the anthers also move asunder, and let fall the floury pollen hitherto wedged between them. A somewhat different mechanism is exhibited by several species of the genus *Pedicularis*, which may be represented by the common alpine *Pedicularis recutita* (fig. 276). The anthers in the flowers of this plant are borne on elastic filaments, and are regularly squeezed between the lateral walls of the helmet-shaped (*galeate*) upper lip. No separation of the valves is possible unless the galeate lip expands and becomes laterally inflated. This is brought about in a very curious manner. When a humble-bee alights it seizes the projecting upper lip and bends it down through an angle of about 30°, this action being facilitated by the presence of strong ribs at the base of the helmet on either side of the throat of the corolla which act like levers, and communicate their motion to the entire upper lip. In consequence of the inclination of the upper lip, the sides of the helmet, which up to this time are tightly stretched, bulge out laterally; secondly, the filaments bend in the same sense as the bulging sides of the helmet; and thirdly, the anthers themselves come apart pouring the

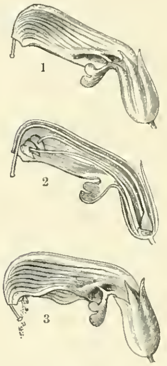


Fig. 276.—*Pedicularis recutita.*

[1] Entire flower. [2] Longitudinal section of the same. [3] Pollen falling out in consequence of the inclination of the helmet-shaped part of the corolla. × 3.

pollen-dust on to the insect's back. In order that this complicated machinery may do its work successfully, the insect must insert its proboscis at a certain definite spot through a little groove in the under lip, and for this reason all other spots where entrance into the flower might be attempted are barricaded. The margin of the upper lip, for instance, is thickly furnished with short-pointed prickles which the insects take care not to touch (*cf.* figs. 276$^{1, 2, 3}$).

The chief points of difference between the kinds of sprinkling apparatus hitherto described and that which occurs in Acanthus flowers (*Acanthus longifolius, A. mollis, A. spinosus*; see figs. 277$^{1, 2, 3}$) are that in the latter the anthers are unilocular instead of bilocular, and that the loculus resembles a long narrow niche rather than the valve of a mussel-shell. Each niche is edged with close short down, a provision which conduces materially to effective closure when the two anthers are in contact. The filaments look as if they were made of ivory; they are unusually strong, and are not so easily pushed asunder. Sturdy humble-bees of large size alone are able to displace these filaments, and the result of their doing so is to part the anthers and cause a shower of floury pollen to descend upon their bodies.

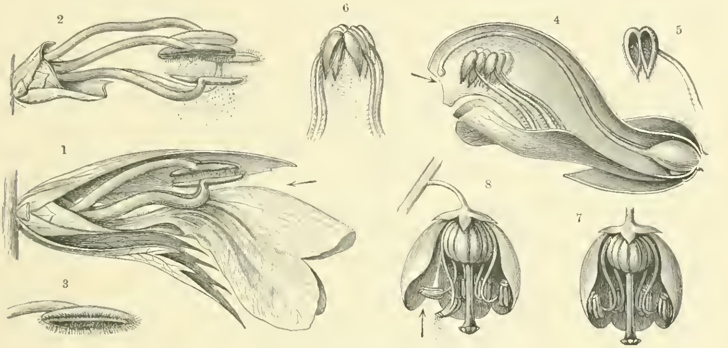


Fig. 277.—Sprinkling apparatus.

^{1} Flower of *Acanthus longifolius* with some of the petals cut away. ^{2} Stamens of *Acanthus* illustrating the sugar-tongs principle; the anthers parted so as to let fall the pollen. ^{3} Single anther of *Acanthus* showing fringe. ^{4} Longitudinal section through the flower of *Rhinanthus angustifolius.* ^{5} Stamen from the same. ^{6} The four stamens of *Rhinanthus* seen from the entrance to flower; the anthers in contact at the top, parted below; the pollen falling out. ^{7} Flower of *Pyrola secunda* with some of the petals and stamens cut away. ^{8} The same; the anther is capsizing owing to the displacement of the petal which has hitherto kept it in position, and pollen is being sifted through the pores. The arrow in figs. ^{1}, ^{4} and ^{8} indicates the direction in which an insect enters the flower. ^{1}, ^{2} natural size; the rest × 2 to 5.

A form of sprinkling apparatus very different from the sugar-tongs variety, with its spoon-shaped anther lobes, is exhibited where the anthers act like pepper-castors. Contrivances of this type occur chiefly in bell-shaped blossoms which are either pendent or nodding. The anthers are furnished at or near their free extremity with two little pores, and are so placed inside the bells as to have the holes facing downwards at the moment when the pollen is to be scattered. The pollen is of a floury consistency and is tightly compressed in the anthers, but it is sifted out intermittently, a little at a time, somewhat as powdered sugar is shaken through the holes of a castor. In some cases the anthers are suspended inside the bells with their pores downwards from the very commencement, as, for example, in the flowers of the Snowflake (*Leucojum vernum*) and those of the Cowberry (*Vaccinium Vitis-idæa*); but in others the elastic filaments are reflexed and hold the anthers at first with their pores upwards, facing the receptacle of the pendent flower. In order that the pollen may fall out of this class of anthers (with pores directed upwards), they must be turned upside down. This inversion is effected by insects, and as an example we will describe how it occurs in a Winter-green (*Pyrola secunda*). The filaments are curved into the shape of the letter S and are in a high state of tension, and the anthers borne by them are held in position, with their pores directed upwards, by the pressure of the petals (see fig. 277 ^{7}). When an insect visits the bell it displaces the petals with the result that the filaments straighten out and the anthers are inverted (fig. 277 ^{8}). In a large number of instances the anthers are furnished with special appendages against which insects are sure to strike when they enter the flower, whereupon a little pollen invariably pours out. The Snowdrop (*Galanthus*) has simple rigid points depending from the free extremities of the anthers and standing in the way of insects, and so also have *Cyclamen*, *Ramondia*, and many other plants belonging to widely-different families. The Strawberry-tree (*Arbutus*) and the Bearberry (*Arctostaphylos*; *cf.* fig. 263 ^{1} p. 240) have two little horns projecting from the back of each anther, against which insects knock in their quest for honey, the result being that the whole anther is shaken and scatters pollen through its pores.

Anthers which dehisce by pores and act in the manner above described are usually associated with actinomorphic (*i.e.* radially symmetrical) and either pendent or nodding flowers, and all the cases we have examined hitherto have in fact been of pendent or nodding bells of perfectly regular conformation. Of the few zygomorphic flowers (*i.e.* symmetrical about one plane only) furnished with anthers of the kind I can only refer briefly to the Calceolariæ and Melastomaceæ. In these plants the anthers rest on short filaments, and are easily set rocking like those of *Salvia*. But whereas in the flowers of *Salvia* the anthers dehisce longitudinally and contain pollen of viscid consistency, those of the Calceolariæ and Melastomaceæ open by pores, whilst the pollen contained in them is of mealy or powdery consistency. The anthers are set swinging by insects knocking against them, and the pores being thus lowered the pollen comes tumbling out on to the bodies of the intruders.

The third form of sprinkling apparatus consists of a whorl of stiff stamens grouped together so as to form a hollow cone. The anther belonging to each stamen is composed of two lobes which open by longitudinal fissures and after dehiscence are simply open niches. The pollen is in the form of meal or powder, and in order to prevent it from falling out of the niches before the right time a special contrivance is necessary to keep them closed. This result is attained by two different methods. According to one method the anther-lobes are pressed firmly against the style round which they stand in a small circle; according to the other the lobes of adjacent anthers face one another and are closed as tightly together as were the anthers of the sugar-tongs-like stamens already described. The first arrangement occurs in *Soldanella* (see figs. $278^{1, 2\ 3}$), the latter in many species of *Erica* and of Boragineæ (see figs. $278^{4, 5, 6, 7, 8, 9, 10}$). In both cases the cone is composed of four or five lanceolate anthers, and the pollen is concealed in eight or ten long narrow loculi which part and let their contents fall if the cone is displaced to the slightest extent. If an insect touches the cone anywhere, as it must do to insert its proboscis, it dislocates the closely-fitting parts and causes a little shower of pollen to descend upon itself. Usually very small quantities of pollen fall at a time. As soon as the proboscis is withdrawn the anthers are replaced in virtue of their elastic filaments, and the same process may be repeated again and again. The insects break into the flowers at various spots; in Heaths (*Erica*) the proboscis is usually introduced through the apex of the cone of anthers, in Borage (*Borago officinalis*; see fig. 278^{7}) at its base. The latter plant is visited by hive- and humble-bees which, alighting on the nodding flowers from below, fasten on with their fore-legs, so that their head and proboscis is brought on to a level with the base of the cone, whilst the hind part of the body is arched under its apex. The insect holds on in this position by a peculiar tooth-like appendage of the filament (see fig. 278^{9}), and with this as a handle pulls the anther of that stamen away from the rest, causing a break in the cone out of which the pollen falls on to the abdomen of the insect as it sucks the honey. In the flowers of several *Boragineæ*—Comfrey (*Symphytum*) and *Cerinthe*, for example—there are peculiar scales, furnished with sharp prickles, alternating with the anthers (see figs. $278^{4, 5, 6}$), and placed in such a position that insects are afraid to insert their

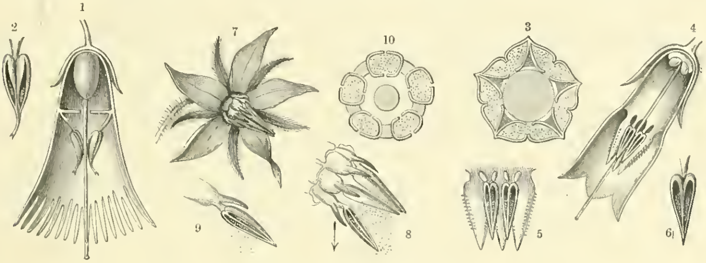


Fig. 278.—Sprinkling apparatus.

[1] Longitudinal section through a flower of *Soldanella alpina*. [2] Stamen from the same seen from that side which is in contact with the style. [3] Diagram of transverse section through the style and the five anthers adherent to it; the lightly shaded part is the style, the darker shaded portions are the connectives, the dotted portions are the pollen. [4] Longitudinal section through a flower of *Symphytum officinale*. [5] Two stamens and three scales of same beset with prickles. [6] Single stamen of *Symphytum*. [7] Flower of *Borago officinalis*. [8] Cone of anthers from the same with one of the stamens bent down in the direction of the arrow, and a little pollen escaping in consequence. [9] Stamen with tooth-like handle on its filament. [10] Diagram of transverse section of the style and anthers of *Borago*; the shaded portions are the style and the connectives of the five anthers, the dotted portion is the pollen. [7] natural size; the rest of the figures × 2 to 5.

probosces except at the apex of the cone of anthers, and in consequence the head alone and not the abdomen is, in this case, besprinkled with pollen. In *Soldanella* (figs. 278 [1] and 278 [2]) the apex of each anther is produced into two little processes. Insects come against them as they enter the flower, with the result that pollen is scattered out of the anthers. Several of the wonderful contrivances which were described on p. 271 as occurring in connection with stamens fashioned like sugar-tongs are also present where the conical arrangement of anthers prevails; and we need not, therefore, discuss the latter at greater length. The only case left requiring special attention is that of the Violet and Pansy (*Viola*, fig. 279 [1]). Unlike the foregoing, the flower in this case is zygomorphic and has its mouth directed sideways, and moreover, the manner in which the anther-cavities, which are full of floury pollen, are moved by insects is peculiar. The cone of anthers is set over the lowest petal, which is prolonged at the back into a spur containing honey. In order to suck the honey an insect must push under the cone and run its proboscis along the channel of the spurred petal. But here it encounters the thickened extremity of the hooked and deflexed style, which it cannot avoid touching and shifting a little. The five stamens forming the cone are closely adherent to the style, so that any displacement of the latter affects them also, and the moment this happens the proboscis of the intruding insect is besprinkled with pollen from the dislocated cone of anthers.

DEPOSITION OF POLLEN.

The pollen which has been taken from one flower has to be deposited in another by honey-sucking insects and birds. How, when, and where the deposition occurs is of great importance, as the transference is in reality the first stage in the series of events leading to fertilization. The stigma is the destination of the pollen, and the right moment for deposition is as soon as the stigma is able to hold fast the pollen which is brought to it. If the pollen is not deposited on the stigma but on some other part of the flower, or if the stigma be dry and shrivelled, and not able to retain the pollen when deposited on it, it is as much wasted as if it had fallen on to the ground or into the water. Hence not only the time and place of deposition, but also the state of the stigma determine exactly the conditions for the success of the transference of the pollen.

If the pollen is scattered on the back of the insect the stigma must come into contact with its back; if it has adhered to the proboscis, the insect must stroke the stigma of the newly-visited flower with its proboscis; if the under surface of its body is covered with pollen, then the stigma will be placed at the bottom of the entrance to the flower, so that the insect must stroke it with its belly. Obviously, then, an insect, whether abstracting or depositing pollen, will follow approximately the same course in the flower, and that position of the anthers most suitable for the shedding of the pollen will, on the whole, be the position most suitable for the stigma to assume in receiving pollen. It might, therefore, have seemed more natural to describe the two processes of abstraction and deposition of pollen together. Both have already been referred to, but a thorough description would have greatly encroached on the account of the transference of the pollen by animals reserved till now, and so it seems more natural to treat the deposition of pollen more particularly here, while connecting it with the processes described above as occasion requires.

In the last chapter, when describing the change of position of anthers and stigmas, it was especially noted that in the flower of the Grass of Parnassus (*Parnassia*; see fig. 267 [4] p. 249) one anther after another placed itself in the centre of the flower, because the road to the honey ran through that part, and the sucking-insects were therefore obliged to remove the pollen from the anther standing in their way. But each anther in turn, as it stands in the centre, covers the stigma which surmounts the egg-shaped ovary, and as long as this is the case, the pollen from another flower cannot be deposited there. It is necessary that the last anther of the series, after giving up its pollen, should move out of the way in order that the stigma may be accessible. This actually occurs; the stigma alone is now to be seen in the place where the five anthers have successively appeared, and when other insects come to suck up the honey, the pollen they bring with them from other flowers is deposited on the stigma. The same sort of thing happens in *Funkia, Centranthus* and *Impatiens*. In the flowers of *Impatiens*, the anthers form a kind of cap which covers the stigma so as to hide it completely when the flower first opens. Only when the cap becomes loose and falls off is the stigma exposed, standing in the place formerly occupied by the anthers. In these cases the position taken up by the stigma at the commencement of flowering is not usually altered, so that it meets the pollen-laden insect in the exact place where the anthers formerly stood. In order to attain this end, however, the styles of most Saxifrages (e.g. *Saxifraga bryoides, cuneifolia, Geum, rotundifolia, stellaris*) as well as the stigmas of many Gentians, and especially those in the revolver-flowers of the Caryophyllaceæ undergo an alteration of position. Originally, the stigmas of these flowers were placed together in the centre, and the pollen-bearing anthers stood in a circle round them; but, after the anthers have fallen and their filaments have shrivelled up, the style splits, that is to say, the stigmas separate from one another and diverge, taking up the position formerly held by the anthers when liberating their pollen.

The styles of Labiatæ undergo still more marked movements, as, for instance, in the Sage (*Salvia glutinosa*), a representative of this order. When the flower first opens only the end of the style projects as a simple point from the edge of the upper lip (see figs. 271 [1] and 271 [2], p. 262, the right-hand flowers). In this stage the humble-bees, entering the flowers, only carry off pollen, and do not touch the top of the style. Later, the style bends down like a bow, and its branches, at first folded together into a single point, separate and place themselves in front of the entrance to the flower, so that the approaching visitors—the humble-bees—must leave on them the pollen they have brought from other and younger flowers (see fig. 271[2], left-hand flowers). A very noticeable change of position of stigmas and anthers is also observed in flowers of the *Gladiolus*, the Hellebore (*Helleborus*), the narrow-leaved Willow-herb (*Epilobium angustifolium*), various species of the genus Honeysuckle (*Lonicera alpigena, nigra, Xylosteum*, &c.), also in the Figwort (*Scrophularia*), species of the genus *Penstemon* and *Cobæa*, and finally in numerous Solanaceæ, as, for example, in the Deadly Nightshade (*Atropa*), the Henbane (*Hyoscyamus*), *Scopolia*, and the Mandrake (*Mandragora*). Looking into the newly-opened flower of the Mandrake (see fig. 279[8]) we see the spherical, sticky stigma close below the entrance and exactly in the centre. The anthers, surrounding it in a circle, are still unopened and placed against the inner wall of the corolla. Since the mouth of the flower at this time is only slightly open, the stamens are scarcely seen. Two days later the appearance of the same flower is greatly altered. The style, bearing the stigma (now pollinated), has bent sideways and impinges on the inner wall of the corolla, the anthers are pushed towards the middle of the now widely-opened mouth, are covered with pollen, and have thus changed places with the stigma (see fig. 279[9]). In the flowers composing the umbels and capitula of many Umbellifers, Scabiouses, and Composites, the anthers and stigmas may be said to change places in a certain sense, since the stigmas do not mature until the neighbouring stamens have shrivelled up, or their anthers have fallen off. In the heads of many Dipsaceæ (*Cephalaria, Succisa*), and the head-like umbels of the *Eryngium*, at first only pollen-covered anthers are seen in all the flowers, and later only the stigma-bearing styles. The insects carry the pollen away in masses from these inflorescences, so it is obvious that the deposition must occur in the same manner, *i.e.* that an insect smothered in pollen, alighting on an inflorescence with numerous stigma-bearing styles, and indulging in a series of lively gyrations attaches its load in a few seconds to dozens of the sticky stigmas.

It is hardly necessary to state in detail that the small-pointed thorns, stiff bristles, and other similar structures by which insects are shown the way into the flower have the same significance for the deposition of pollen on the stigma as for its removal from the anthers, and we can now merely refer to the descriptions on pp. 250, 271, and 275. Only one other contrivance especially connected with the deposition of pollen on the stigma, which acts as a remarkable sign-post, need be mentioned here. In the flowers of many Cruciferæ, *e.g.* those of *Kernera saxatilis*, whose first and last stages of development are shown in figs. 267[8] and 267[10], p. 249, the petals at the time of opening are still small, stand erect, or are even somewhat inclined inwards, almost touching the large stigma which nearly fills up the entrance to the flower. Insects wishing to suck the honey at the base of the flower are obliged by this position of the petals to push their probosces down close by the stigma. Should the proboscis have been loaded with pollen in other flowers, this will be inevitably deposited on the stigma. Later, when the stigma is withered, and the floral-leaves have enlarged, the whole flower becomes inflated, the floral-leaves becoming concave inwardly, the pollen-covered anthers become visible and accessible; and now when an insect directs its proboscis to the base it no longer touches the stigma, but brushes off the pollen from the anthers. The same arrangement is repeated with but little deviation in the flowers of the Asarabacca (*Asarum*). The opening of the perianth in this flower begins with the appearance of three fissures between the three perianth-lobes, and these serve as entrance-gates for the small flies seeking access to the interior of the flower (see fig. 279 ^{12}). The stigmas which are to be pollinated are close below the three fissures, and the insects using them as entrance-gates must of necessity pass over the stigmas. If they come laden with pollen from an older flower they cannot avoid leaving a portion behind on the stigmas. Later, when the stigmas are pollinated, the three perianth-lobes separate at the tips also, where they have hitherto been joined together (see fig. 279 ^{13}). It is then no longer necessary that the insects should be shown the way to the stigmas.

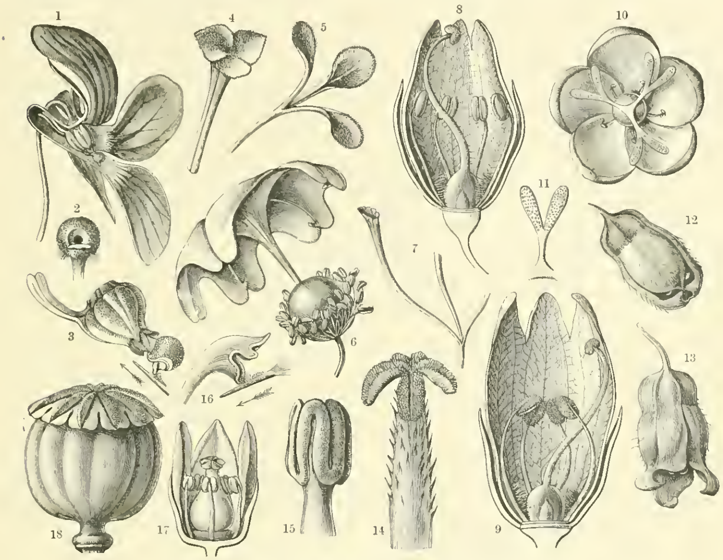


Fig. 279.—Arrangements for the Retention of the deposited Pollen.

^{1} Flower of the Violet (*Viola odorata*); part of the corolla cut away. ^{2} Capitate end of the style of this flower seen from underneath. ^{3} Pistil of the Violet surrounded by the cone of anthers; pollen is deposited on the small lip of the capitate stigma by the proboscis passing in the direction of the arrow. ^{4} Stigma of the Narcissus (*Narcissus poeticus*) with finely toothed margin. ^{5} Stigma of Gladiolus (*Gladiolus segetum*) with ciliated edges. ^{6} Pistil of *Sarracenia purpurea*; the ovary surrounded by the stamens. ^{7} Funnel-shaped stigma of the Crocus (*Crocus sativus*); one of the three stigmas only remaining. ^{8} Flower of the Mandrake (*Mandragora vernalis*) in the first stage of blossoming. ^{9} The same in the later stage of blossoming. Part of the corolla and calyx cut away. ^{10} Flower of the Sundew (*Drosera longifolia*) seen from above. ^{11} Part of the sticky papillose stigma of the Sundew. ^{12} Flower of the Asarabacca (*Asarum Europæum*) in the first stage of blossoming. ^{13} The same flower at a later stage. ^{14} Stigma of *Roemeria*. ^{15} Stigma of *Opuntia nana*. ^{16} Stigma of *Thunbergia grandiflora*; pollen is deposited on the lower lip by a proboscis passing in the direction of the arrow. ^{17} Flower of *Azalea procumbens*; portions of the calyx and corolla cut away. ^{18} Pistil of the Opium Poppy (*Papaver somniferum*). ^{6} and ^{18} natural size; the others somewhat enlarged.

No less important than the position of the stigma and its relation to the rest of the flower is its capacity for retaining the pollen brought to it. As might be expected, flowers which are visited by insects agree but slightly in this respect with those which are wind-pollinated. In all the instances where the pollen collected by insects or birds has to be brushed off in adhesive crumbling masses, delicate feathery stigmas, such as those of Grasses and many other plants which receive powdery pollen by wind agency, would be of no use; but to the former, stigmas possessing projecting edges, bands, and lobes, on which the insects as they pass must leave their pollen, are better adapted. Usually close to the projecting edge there is a depression which is filled with the deposited pollen. Thus, for example, the style of *Thunbergia* (see fig. 279^{16}) ends in a funnel-shaped stigma whose edge projects on one side like a shovel. When an insect strikes against this stigma on entering, the pollen is received by this shovel and is at once deposited in the funnel-shaped depression. Insects which push their probosces into the flowers of the Violet (*Viola*) inevitably strike against a little flap projecting from the lower side of the capitate stigma (see figs. $279^{1, 2, 3}$), and when the proboscis is covered with pollen this is left adhering to the inner side of the lobe. When the insect withdraws its proboscis the lobe is pressed back against the stigmatic head, and thus the recently received pollen is pushed into its cavity. The flowers of Irises possess stigmas with the shape and colour of petals. They are bilabiate at their free end (see figs. 265^1 and 265^2, p. 246). The upper lip of the stigma is curved, fairly large, and split into two points, the lower lip is thin and forms a narrow membraneous lobe spread out transversely. The path traversed by the humble-bee in obtaining the honey passes under one of the bilabiate stigmas, and when it comes laden with pollen from another flower it pushes down the thin flap of the lower lip, so that the pollen is brushed from its back and deposited between the two lips. Many Scrophulariaceæ and Lentibulariaceæ (*Catalpa, Mimulus, Rehmannia, Torenia,* and *Utricularia*), of which the Monkey-flower (*Mimulus luteus,* see figs. $280^{1, 2, 3}$), may serve as a type,

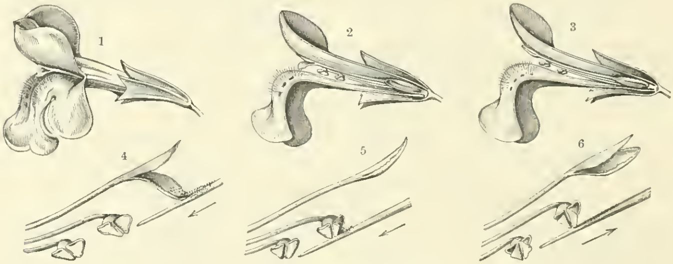


Fig. 280.—Deposition of the Pollen.

[1] Flower of the Monkey Flower (*Mimulus luteus*). [2] The same flower cut in half lengthwise with open stigma. [3] The same flower with closed stigma. [4] Pollen is deposited on the lower lip of the stigma by a proboscis passing in the direction of the arrow. [5] The stigma has closed in consequence of the stimulation: the proboscis passing in the direction of the arrow opens the closed anthers and loads itself with pollen. [6] The lower lobe of the stigma is only slightly raised so that it does not come into contact with the proboscis which is being withdrawn in the direction of the arrow, and consequently the pollen adhering to it does not reach the stigma. ^{1}, ^{2}, and ^{3} natural size; the others somewhat enlarged.

have bilabiate stigmas which exhibit sensitive movements. When the pollen is deposited by an insect on the lower lip of the stigma, which stands in its way as it enters (280^4), the two lips immediately close together like the leaves of a book (280^5), and thus the pollen is carried to that part of the stigma where it undergoes further development. When the insect withdraws its proboscis there is no chance of the pollen which it is taking from the anthers getting into the interior of the stigma, since the stigma is still shut up and no longer stands in the way of the insect (280^6). The stigma of *Mimulus luteus* remains closed after being stimulated with a needle for about five minutes; when it again opens, the lower lip resuming its former position, it may be again closed if further stimulated. In other species of the genus, as also in *Martynia* and *Catalpa*, the same phenomenon is observable. None of the previously-mentioned plants appear to keep their stigmas closed more than two minutes. This repeated opening of the stigma is very important in case the first insect visiting the flower should have brought no pollen with it. Since the stigma opens again it has apparently some expectation of a second visit. Should this also be unsuccessful it may open a third time. The opening and closing usually continue until at length an insect deposits pollen on the stigma. When this happens the stigma, though opening yet again for a brief period, remains permanently closed so soon as the influence of the pollen is felt.

The contrivances described above are based on the fact that the pollen stroked off the visiting insects by the projecting edges, bands, and lobes, is conducted from them to the portion of the stigma adapted to receive it. To this first group of contrivances for retaining pollen may be added another where the insect on entering into the base of the flower leaves the pollen it has brought on the papillose, superficial cells of the stigma. This occurs, for example, in the flowers of Malvaceæ and Caryophyllaceæ, the styles of which are studded with long tube-like papillæ; they act like brushes. In the flowers of the Rock-rose (*Helianthemum*), and in those of the Day-Lily (*Hemerocallis*), long papillæ are grouped paint-brush-wise on the capitate stigma, but most frequently the trimming of very numerous long and crowded papillæ has the appearance of velvet, and such stigmas are termed "velvety" by descriptive botanists. The genera *Erythræa, Daphne,* and *Hibiscus* may be mentioned as well-known plants with velvety stigmas. In many plants the stigmatic papillæ are but slightly prominent, the surface appearing rough, irregular, or granulated. If the flowers are crowded, and the deposition of pollen occurs simultaneously on numerous stigmas, these are usually linear or only beset with papillæ on one side, as in *Cephalaria*, or clothed all over, as in *Armeria*, but always so formed and placed that the insect moving over the flower-head may rub off its pollen as easily and quickly as possible on to the stigmas. In those plants where the stigma rising in the middle of an erect, shallow flower is used as a resting-place by the insect, either the whole surface is thickly beset with papillæ (*e.g.* in *Roemeria*, fig. 279^{14}), or they are arranged in the form of rows distributed in radial lines, as in the Poppy (*Papaver*, fig. 279^{18}). It frequently happens that the papillæ only border the edge of the stigma, resembling eyelashes on an eyelid, or the teeth of a comb. This is particularly the case if the stigma is lobed, the lobes being fairly large and spoon-shaped, cup-shaped, or like a funnel, and if the insect on entering only touches the edge of the stigmatic lobes with the pollen-laden part of its body. This is the case, for example, in the flowers of many Gentians, Narcissi, Gladioli, and Crocuses (e.g. *Gentiana Bavarica, Narcissus poeticus, Gladiolus segetum, Crocus sativus*; *cf.* figs. $279^{4, 5, 7}$).

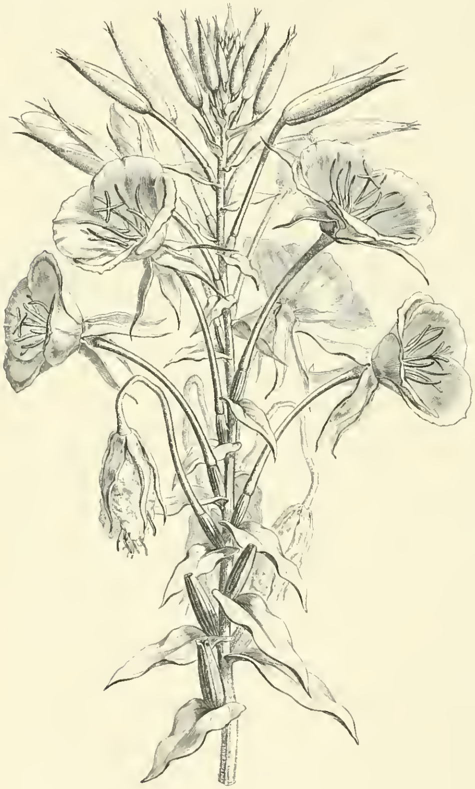


Fig. 281.—Evening Primrose (*Œnothera biennis*). (After Baillon.)

The pollen, when deposited, is held between the papillæ of the stigma like dust on velvet pile or on a brush or comb; nor is it absolutely necessary that the stigmatic papillæ should be sticky, though, of course, the power of retention is thus obviously increased. Some stigmas are beset with transparent papillæ, and at the same time are rendered very sticky by a layer of fluid secreted by the surface cells of the stigma, as, for example, in the Sundew (*Drosera*; *cf.* 279^{10} and 279^{11}). But such cases are rare on the whole. Usually the velvety stigmas and those beset with long papillæ are not sticky, the viscosity being restricted to wart-like and granulated stigmas. Examples of plants with very sticky stigmas are furnished by the Umbelliferæ, the Rhododendrons, Bearberries, Ericas, Whortleberries and Cranberries, Winter Greens and Polygonums, the Deadly Nightshade, and Bartsias. A sticky stigma often terminates a thin threadlike style either as a small disc or head, and is the more conspicuous on account of the glitter of its sticky coating than because of its size. In the flower of the Mahogany-tree (*Swietenia Mahagoni*; see fig. 282^{3}) it has the form of a disc, in *Azalea procumbens* (see fig. 279^{17}) it is slightly convex with five projecting ridges radiating from the centre, in the Prickly Pear (*Opuntia*; see fig. 279 [15]) it forms a sinuous fleshy swelling which winds about the end of the style, whilst in the Evening Primrose (*Œnothera*; fig. 281) it is composed of four fleshy lobes arranged in a cross. It is noticeable that sticky stigmas occur most frequently in plants whose pollen is liberated from the sprinkler-like anthers as flour or dust. Such flowers also, the pollen of which consists of quartets (tetrads) of cells surrounded and entangled in delicate threads, are characterized by very sticky stigmas (*cf.* fig. 219 [2], p. 101). In most of the plants mentioned above the pollen adheres so firmly to the stigma at the moment of contact that it cannot be removed even by blowing or vigorous shaking. Many of the sticky stigmas remind one of limed twigs, especially as the sticky layer which produces the adhesiveness is exposed to the air and yet does not dry up, but remains sticky and viscous like bird-lime for several days.

In many instances the stigma does not become sticky until the stigmatic tissue is capable of inciting the pollen-cells which come in contact with it to put out pollen-tubes. The stigma of *Cephalaria alpina*, one of the Dipsaceæ, is very remarkable in this respect. Shortly after the corolla has opened, the stigma appears to be completely matured, and as if capable of retaining pollen. But this is not really so. Any pollen placed on it immediately slides off its smooth surface. Not until two days later when the stigmatic tissue has become covered with a delicate layer of sticky fluid, scarcely visible to the eye, is the pollen held fast, and at once puts out pollen-tubes which penetrate into the tissue. But, as in so many other cases, it is impossible to generalize on this point, thus in most Umbelliferæ the stigmas are sticky before their tissue is able to influence the pollen in this way. Also, in the flowers of *Allium Victorialis*, the pollen adheres to the stigmas before these are capable of inciting the emission of pollen-tubes, indeed, at the time of attachment the stigmatic papillæ are not even developed. The stigmas of Orchids are sticky some time before the ovules are matured. In these cases the sticky layer has to retain the pollen until the changes have been completed in the deeper stigmatic tissue which will stimulate the pollen to put out its tubes.

It is necessary to give a special description of the manner in which the pollen is deposited on these sticky Orchid stigmas. The stigma of the Helleborine (*Epipactis latifolia*), illustrated in fig. 268, p. 255, has the form of a rectangular table, and is placed opposite the boat-like labellum, which is filled with honey. When a wasp, in licking out the honey, strikes its head against the projecting rostellum at the upper margin of the stigma it adheres for a moment. The two club-shaped masses of pollen which are connected with the rostellum are thus torn out of the loculi of the anthers, and removed by the wasp as it flies away. The wasp now carries the pair of pollen-masses on its head as shown in fig. 268 [6]. At first these pollinia stand erect, but after a few minutes they alter their position. In consequence of drying, the masses, composed of adhering groups of pollen-cells, twist and become deflected, and now appear as two thick cushions lying on the front of the head (see fig. 268 [7]). This bending is absolutely necessary if the pollen is to be brought by the wasp to the sticky stigma of another flower. If the wasp came with erect pollen-masses to lick up the honey they would be knocked off by the rostellum, and their aim would either fail entirely or be but partially achieved. But, as soon as the little clubs have bent down over the front of the wasp's head, they are planted by this honey-licking insect exactly on the sticky rectangular stigmatic surface. Each quartet of pollen-cells forms a round or irregularly rectangular ball, and these, connected together by viscous threads, are again grouped so as to form the club-like pollen-mass. When this club is placed on the sticky stigma, all the pollen-quartets which come into contact remain attached, so that when the insect flies away it is much more likely that the sticky threads in the interior of the pollen-mass will be torn than that the pollen adhering to the stigma will be removed again. These two contrivances, so important for the deposition of the pollen on the stigma, viz. the twisting and bending of the originally erect pollen-masses and the tearing of the fine threads which connect the quartets of pollen-cells, occur not only in the Helleborine (*Epipactis*), which has been chosen as an example, but also in many other Orchids which adorn our woods and meadows—especially in the genera *Orchis*, *Gymnadenia*, and *Habenaria*. In the *Epipogium* (see fig. 257, p. 226) the floral contrivances are rather different. Each pollen-mass is chained on one side by the thick strand which leads to the sticky rostellum (fig. 257 [11]). When these masses are torn from their hiding-place by a humble-bee (257 [13]) they bend round, and now hang on their supports like two cherries on their stalks. In this way the structure, torn from the anther, becomes somewhat elongated—an important change—since it renders it possible that the clubs should reach the stigma in the next *Epipogium* flower visited. In this plant the stigma stands above the rostellum, and the pollinia can only be pressed by flying humble-bees against the stigma if they have long stalks.

Each of these contrivances shows afresh how exact must be the correlation of all the organs which participate in the transference of pollen, and how well they must be regulated if the success of the flower is to be ensured. The alteration of a millimetre in the position of the stigma will prevent the pollen being deposited on the right place and the consequent fertilization. In many cases a still slighter alteration would be hurtful. In some plants only a very limited area of the stigma is able to incite the pollen to emit pollen-tubes. In Asters, as will be shown more in detail presently, it is only a narrow border at the edge of the minute stylar branch, and in many Labiatæ it is only the tip of the lower branch of the stigma on which pollen can be deposited with successful results. *Sarracenia purpurea* possesses one of the largest stigmas. It has the form of a sunshade of 3·5 cm. diameter, with five indented lobes round the edge, and the margin of each lobe is furnished with a small tooth on the inside (see fig. 279 [6]) These teeth alone are fitted to receive pollen, and if the term stigma is to be restricted to the tissue on which the pollen can eventually develop and put out pollen-tubes, it will only refer in *Sarracenia* to these five tiny teeth. The same is true of *Physostigma venenosum* (see figs. 282 [1] and 282 [2]) whose bladder-like stylar termination, described as the stigma, is only capable of real pollination over a small part beset with papillæ. It should also be noted here that the papillæ which are developed on the outer side of the stylar branches in Compositæ, and which at first sight might be mistaken for stigmatic papillæ, do not deserve this appellation. Their function is only to sweep the pollen out of the anther-tube, and their significance will be repeatedly spoken of later in the chapter devoted to autogamy.

The deposition of pollen on the stigma is followed not only by alterations in the pollen-cells and in the stigmatic tissue, but also in other parts of the flower, especially the corolla. The visible changes in the stigma are the withering, shrivelling, and turning brown of its superficial cells. In those plants described above, on whose sticky stigmas the pollen is not immediately stimulated to send out pollen-tubes, weeks sometimes elapse before these alterations occur; in others, however, they are to be observed in a few hours. Solanaceous plants are very noticeable in this respect, especially *Nicandra physaloides*, and the Deadly Nightshade (*Atropa Belladonna*). An hour after pollen is deposited on the sticky stigma, it begins to wither and turn brown, and the whole style alters and drops off the ovary. Here, then, the pollen-tubes must have been emitted as soon as the pollen-cells came in contact with the stigmatic tissue, and they reach the ovules in the interior of the ovary within a few hours.

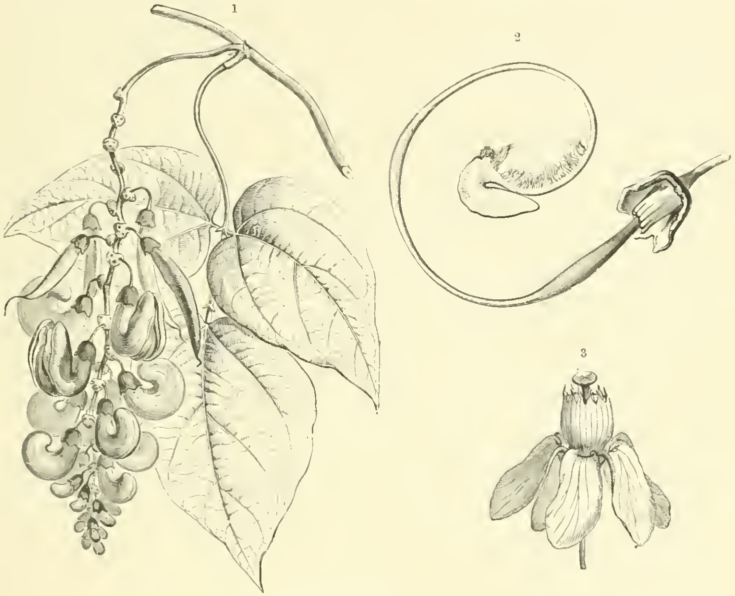


Fig. 282.—^{1} *Physostigma venenosum.* ^{2} Pistil of this plant, removed from the flower; magnified. ^{3} Flower of *Swietenia Mahagoni.* (After Baillon.)

The changes which occur in the petals are even more noticeable. As soon as the stigma is withered they begin to wither also, or they become detached from the flower and fall off. The withering of the petals occurs in very many ways. They lose their turgidity, shrink up, occupy less space, and at the same time change their colour. A change takes place in the petals of most flowers which last only a day, a change similar to that which occurs in foliage-leaves which have passed through a sharp night frost in autumn and then been exposed next day to the sun—*i.e.* they exude water from their tissue and become pulpy and look as if they had been squashed or boiled. The corollas of some Papilionaceæ, especially several species of the Clover genus (*Trifolium*), dry up and rapidly become like withered leaves. The mean between these two instances is furnished by those numerous plants whose flowers become limp, shrink up somewhat, bend over, and then when withered fall off, as, for example, in most Cruciferæ, Valerians, and Compositæ. The petals in withering often assume the position which they occupied originally in the bud. Thus, for example, the tongue-shaped flowers of the Goat's Beard (*Tragopogon*) roll together into a tube on withering, and thus have the same appearance as just before blossoming. Of course this is not always the case, for the tongue-flowers of *Bellidiastrum* and of most Asters roll spirally outwards when they fade, those of *Hieracium staticefolium* spirally inwards, and it is not rare for fading, drying, and discolouring petals to undergo corkscrew-like torsions. The connection between the withering and the discoloration which accompanies it has already been mentioned (p. 222). In many plants it happens that petals drop from the flower either singly or all together after the deposition of pollen on the stigma without having previously withered at all. Examples are furnished by Roses, Almonds, Primulas, and Fuchsias.

It has been repeatedly shown by researches instituted for the solution of the question that the sudden withering and falling of the petals is really dependent on the deposition of pollen on the stigma, *i.e.* on the penetration of pollen-tubes into the stigmatic tissue. If of two flowers which open simultaneously one is provided with pollen and the other is shielded from it, or rather if the stigma of one flower is purposely pollinated while the other is guarded from the deposition of pollen, the latter will last longer and will not fall as soon as the former. In two blossoms of a Flax (*Linum grandiflorum*), which opened at the same time and were treated in this way, the corolla remained 35 hours on the flower whose stigma was pollinated, but 80 hours on the other flower whose stigma had received no pollen. Of two flowers of *Anagallis Philippi* the corolla fell in four days from the one which had been pollinated, but remained for six days on the flower whose stigma had been protected from pollen. In a plant of *Mammillaria glochidiata* the flowers which were pollinated appeared pulpy and permanently closed two days before those whose stigmas remained free from pollen. Orchids as cultivated in hot-houses offer a very well-marked example of this same property. Normally these flowers are free from insect-visits in the hot-house and their flowers remain fresh for many days, and in some instances for weeks. If, however, the stigmas of these same plants be artificially pollinated, a quick collapse of their showy perianths is observed. If the view that the gaily-coloured corollas act primarily as allurements to insects which visit flowers and transfer pollen require strengthening these results are certainly found to be in accordance. As soon as the end is gained, *i.e.* as soon as the stigma is pollinated, the further allurement of insects is unnecessary; the petals therefore immediately cease working, fall off or wither, and are no longer divergent—in a word, they have ceased to act as an allurement to insects. This phenomenon can only be explained by supposing that the changes produced in the tissues of the stigma by the developing pollen-grains take effect in ever-widening circles which at length reach the petals, and that by what we may term the stimuli, transmitted from the stigmatic tissue and the ovary to the corolla, a sudden separation between the petals and the rest of the flower and an equally sudden alteration in the turgidity of the petals are brought about.

It only remains to be mentioned that the early withering and fall of the petals of those flowers which are pollinated soon after opening has a counterpart in the phenomenon of the long duration of double flowers. Double flowers, in particular those whose stamens and carpels have been transformed into petals, remain fresh two, three, even eight days longer than the normal single flowers of the same kind, as may be seen, for example, in Pelargoniums, Tulips, Pinks and Stocks.

THE CROSSING OF FLOWERS.

While Goethe was staying at Carlsbad a young gardener every day brought him a bunch of flowering plants from the visitors assembled at the waters and undergoing the cure. Both men and women were greatly interested in ascertaining the names of these plants with the assistance of the writings of the Swedish botanist Linnæus, whose fame had at that time spread far and wide. This searching for names was called the "naming" or "determining" of plants, and it was prosecuted with great zeal by dilettanti as a sort of puzzle-game and as a pleasant, stimulating pastime. Even in professional circles Linnæus found a recognition which has rarely been accorded to a contemporary. His method had taken the whole world by storm, and his "system" was everywhere in the ascendant. Of course individual voices were raised against the new teaching, chiefly indeed from the dilettanti. Goethe relates that many of the Carlsbad visitors designated the pursuit of the knowledge of the Vegetable Kingdom according to the Swedish botanist as senseless play which satisfied neither the understanding nor the imaginative faculty, and could relieve no one of ennui. Evidently Goethe also had perceived the weakness of the Linnean method. Besides, he was not concerned with counting or numbers nor the distinction of forms founded on insignificant points; he was not interested in the differences of plants, but rather in what they had in common and in what bound the

Vegetable Kingdom into a many-membered whole. It is therefore obvious that he could never have felt much enthusiasm for the Swedish botanist.

But, strange as it may sound, that which Goethe regarded as the weak point in the Linnean system was, on the contrary, its strength. The very fact that counting afforded a safe path through the apparent chaos of plant-forms, that by means of counting the floral parts the possibility was afforded of attaining to a short and intelligible classification; and not least, the persistent adherence to the principles laid down fascinated both lay and professional men. These same good points explain why even many quite recently issued works (tourists' pocket-floras and the like) retain the Linnean system when their object is to facilitate a speedy reference of a plant to its position amid the plexus-like ramifications of the phylogenetic tree. Later on we shall have an opportunity of investigating the value of the different plant-systems from an historical standpoint. Here the Linnean system claims our attention solely on the ground of the division of the stamens and pistil, *i.e.* of those organs in which the two kinds of sexual cells are formed. The results of the researches into the divisions of these organs in which the fertilizing and receptive sexual cells, *i.e.* the male and female cells are developed, form the foundation of the Linnean system and afford the most important marks for the division into the so-called Classes, of which Linnæus distinguished twenty-four.

The first 20 classes of the Linnean system include Phanerogams, whose flowers are all hermaphrodite, *i.e.* in which each flower of the plant contains both stamens and pistil. Those species whose stamens are all the same length, and are neither joined to one another nor to the pistil, are all in the first 13 classes. Each of these 13 classes is distinguished in the following manner:—

CLASS.

1. MONANDRIA. A single stamen in each flower; *e.g.* Mare's-tail (*Hippuris*), Indian Shot (*Canna*), *Alpinia* (see fig. 283 [1]).
2. DIANDRIA. Two stamens in each flower; *e.g.* Speedwell (*Veronica*; see fig. 257 [1]), Lilac (*Syringa*; see fig. 283 [2]).
3. TRIANDRIA. Three stamens in each flower; e.g. *Iris* (see fig. 265, p. 246), Valerian (*Valeriana*; see fig. 283 [3]).
4. TETRANDRIA. Four stamens in each flower; *e.g.* Woodruff (*Asperula*), Plantain (*Plantago*), Cornel (*Cornus*; see fig. 283 [4]).
5. PENTANDRIA. Five stamens in each flower; *e.g.* Deadly Nightshade (*Atropa*), Cowbane (*Cicuta*), *Aralia*; (see fig. 283 [5]).
6. HEXANDRIA. Six stamens in each flower; *e.g.* Tulip (*Tulipa*), Lily of the Valley (*Convallaria*), *Gagea* (see fig. 283 [6]).
7. HEPTANDRIA. Seven stamens in each flower; *e.g.* Horse Chestnut (*Æsculus Hippocastanum*; (see fig. 283 [7]).
8. OCTANDRIA. Eight stamens in each flower; *e.g.* Ling (*Calluna*), Spurge Laurel (*Daphne*; see fig. 283 [8]).
9. ENNEANDRIA. Nine stamens in each flower; *e.g.* Bay Laurel (*Laurus*), Flowering Rush (*Butomus*; see fig. 283 [9]).

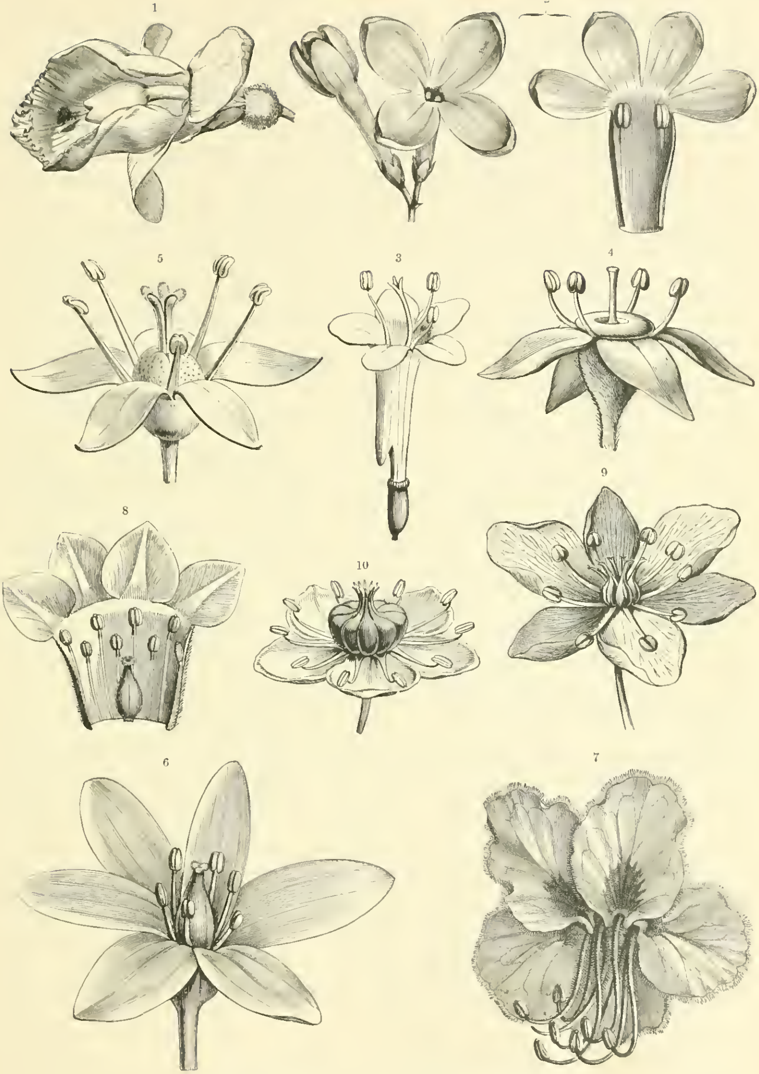


Fig. 283 —Types of the 1st to 10th classes of the Linnean System.

[1] *Alpinia* [2] *Syringa vulgaris.* [3] *Valeriana officinalis.* [4] *Cornus mas.* [5] *Aralia Japonica.* [6] *Gagea lutea.* [7] *Æsculus Hippocastanum.* [8] *Daphne Mezereum.* [9] *Butomus umbellatus.* [10] *Phytolacca decandra.* All the flowers somewhat enlarged.

CLASS.

10. DECANDRIA. Ten stamens in each flower; *e.g.* Rue (*Ruta;* see fig. 290), *Phytolacca* (see fig. 283 [10]).

11. DODECANDRIA. Number of stamens not quite definite, 11–20 in each flower; *e.g.* Mignonette (*Reseda*), House-leek (*Sempervivum*), Agrimony (*Agrimonia Eupatoria*; see figs. 285 [1] and 285 [2]).

12. ICOSANDRIA. More than twenty stamens in each flower, situated on the edge of the cup-shaped receptacle (or calyx-tube), their position, therefore, being *above* or *on a level* with the stigma; *e.g.* Rose (*Rosa*), Almond (*Amygdalus*), *Calycanthus;* see fig. 285 [3]) *Chrysobalanus* (see fig. 285 [4]).

13. POLYANDRIA. 20–200 stamens in each flower, springing from the receptacle *below* the pistil; *e.g.* Poppy (Papaver), Lime (*Tilia;* see figs. 284 [1] and 284 [2]) and *Anemone* (see fig. 284 [3])

In the 14th and 15th Classes Linnæus puts all Phanerogams with hermaphrodite flowers in which the stamens are unequal in length.

14. DIDYNAMIA. Includes flowers with four stamens, two long and two short; *e.g.* the Foxglove (*Digitalis*), Snapdragon (*Antirrhinum;* see fig. 284 [6]).

15. TETRADYNAMIA. Includes flowers with six stamens, four long and two short; *e.g.* Mustard (*Sinapis*), Wall-flower (*Cheiranthus*), Bitter-cress (*Cardamine;* see figs. 284 [7] and 284 [8]).

The 16th–20th Classes include all Phanerogams whose stamens are joined in any way either to one another or to the pistil. They are distinguished from one another thus:—

16. MONADELPHIA. The filaments of all the stamens of a flower are joined into a tube; *e.g.* Tamarind (*Tamarindus Indica;* see fig. 284 [9]), Hollyhock (*Althæa*), Mallow (*Malva*), Baobab (*Adansonia;* see fig. 284 [10]).

17. DIADELPHIA. The filaments of the stamens are united and form two groups; *e.g.* Milkwort (*Polygala*), Fumitory (*Fumaria;* see figs. 285 [5] and 285 [6]).

18. POLYADELPHIA. The filaments of the stamens are united and form three or more groups; *e.g.* St. John's Wort (*Hypericum*), *Melaleuca;* (see figs. 284 [4] and 284 [5]).

19. SYNGENESIA. The anthers of the stamens in each flower are joined together into a tube; *e.g.* in *Lobelia,* Hawkweed (*Hieracium;* see figs. 222 [4] and 222 [7], p. 112).

20. GYNANDRIA. The stamens are united with the pistil; *e.g.* the Orchids: *Phalænopsis,* (see figs. 258 [1] and 258 [2], p. 227); *Cypripedium* (see figs. 267 [1] and 267 [2], p. 249); *Epipactis;* see figs. 268 [2] and 268 [3], p. 255); also the Birthwort (*Aristolochia;* see figs. 284 [11] and 284 [12]).

Now come those plants whose flowers are not hermaphrodite or not all hermaphrodite, and these are distinguished in the following way:—

21. MONŒCIA. Flowers monœcious, *i.e.* the flowers which contain only stamens or only pistils, are separated but grow on the same plant, *e.g.* the Maize (*Zea Mais*), the Oak (*Quercus;* see fig. 286); the Castor-oil Plant (*Ricinus;* see figs. 285 [7] and 285 [8]), *Croton* (see figs. 285 [11] and 285 [12]), *Liquidambar* (see figs. 285 [9] and 285 [10]).

22. DIŒCIA. Flowers diœcious, *i.e.* the flowers containing stamens only are found on certain plants, and those with pistils only on other plants; *e.g.* the Willow (*Salix;* see fig. 287).

23. POLYGAMIA. Flowers polygamous, *i.e.* staminate, pistillate, and hermaphrodite flowers are all found either on the same or on different plants, in various ways; *e.g.* the Ash (*Fraxinus;* see fig. 230, p. 138).

24. CRYPTOGAMIA. Includes Non-flowering Plants.

Linnæus described 20 out of the 23 Classes of Phanerogams as hermaphrodite. He considered hermaphrodite flowers generally to be the rule, and thought them more complete than the unisexual. He connected their prevalence directly with the formation of fruit, and believed the presence of stamens and pistils in the same flower could be explained most simply and naturally by the fact that fertilization could be performed much more easily when the receptive and fertilizing organs were in immediate proximity than when they were widely separated, and thus the formation of seeds capable of germination be best ensured. In a word, the idea originated and found expression afterwards as an actual doctrine that fertilization begins in hermaphrodite flowers by the transference of the pollen on to the stigma of the same flower, *i.e.* that the process occurs which we now call *autogamy* or self-fertilization. More recent researches, however, have shown that many plants are only apparently (or pseudo-) hermaphrodite; that stamens and carpels indeed stand close together in their flowers, but that the pollen-grains in the anthers are not properly developed and have lost their fertilizing capacity. In other flowers, regarded as hermaphrodite, the ovules are so altered that they are unable to develop into seeds capable of germination. It has also been shown that plants provided with both unisexual and hermaphrodite flowers, which Linnæus called polygamous and placed in the 23rd Class, occur much more frequently and in much greater variety than was formerly supposed. There is a long series of forms, one limit of which is constituted by plants with truly hermaphrodite flowers, and the other by diœcious plants. It is impossible, for want of space, to give an exhaustive description of all the members of this series; but since it is important, for the sake of what follows, to obtain as clear an idea as possible of this matter, the chief members of the series at any rate will now be enumerated.

At one end of the series, then, are the bisexual flowers. They always contain one or several stamens besides the ovary. In the ovary are developed the ovules which after successful fertilization become seeds capable of germinating; whilst the anthers of the stamens contain pollen grains which have the power of fertilizing. These flowers are termed *hermaphrodite* and it is desirable to emphasize the expression by speaking of them as truly hermaphrodite flowers.

The unisexual flowers come next. In these only one of the two sets of organs which take part in fertilization is fully matured and able to perform its function. When only the pistil is present, with ovules capable of development, and the stamens do not mature or are entirely absent, the flowers are called female or pistillate; flowers which contain stamens only, with fertile pollen, whose pistil does not mature or is altogether absent, are termed male or staminate. Four kinds of unisexual flowers may be distinguished: (1) Pistillate flowers which appear hermaphrodite. In these pistil and stamens are present, and these flowers therefore seem at first sight to be bisexual. Their pistil contains ovules which can be fertilized and are capable of development, but the cells which are formed in the tissues of the anthers have no fertilizing power. (2) Staminate flowers which appear hermaphrodite. These are the counterpart of the first group. They also contain both

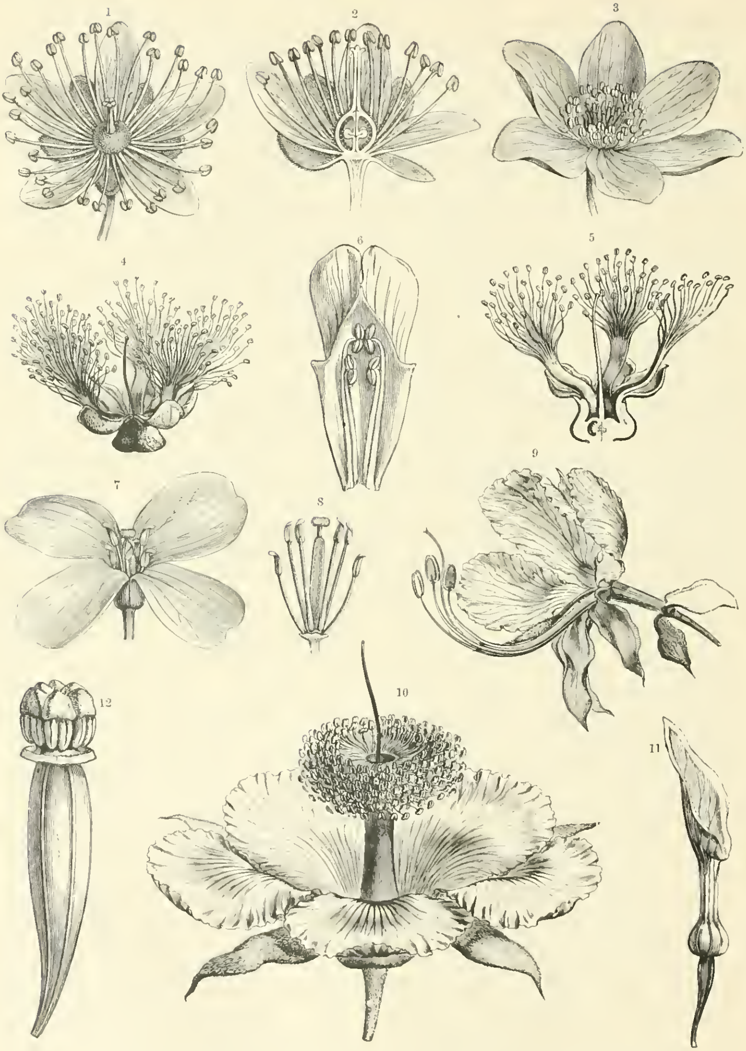


Fig 284.—Types of the 13th, 14th, 15th, 16th, 18th, and 20th classes of the Linnean System.

1, 2 *Tilia*, whole flower and section of same. 3 *Anemone nemorosa*. 4, 5 *Melaleuca*, whole flower and section of same. 6 *Antirrhinum*, upper lip of corolla showing stamens. 7 *Cardamine pratensis*. 8 The same flower, the petals removed. 9 *Tamarindus*. 10 *Adansonia*. 11 *Aristolochia Clematitis*. 12 The same flower after removal of the perianth. 6, 9, 10, 11 natural size; the others somewhat magnified.

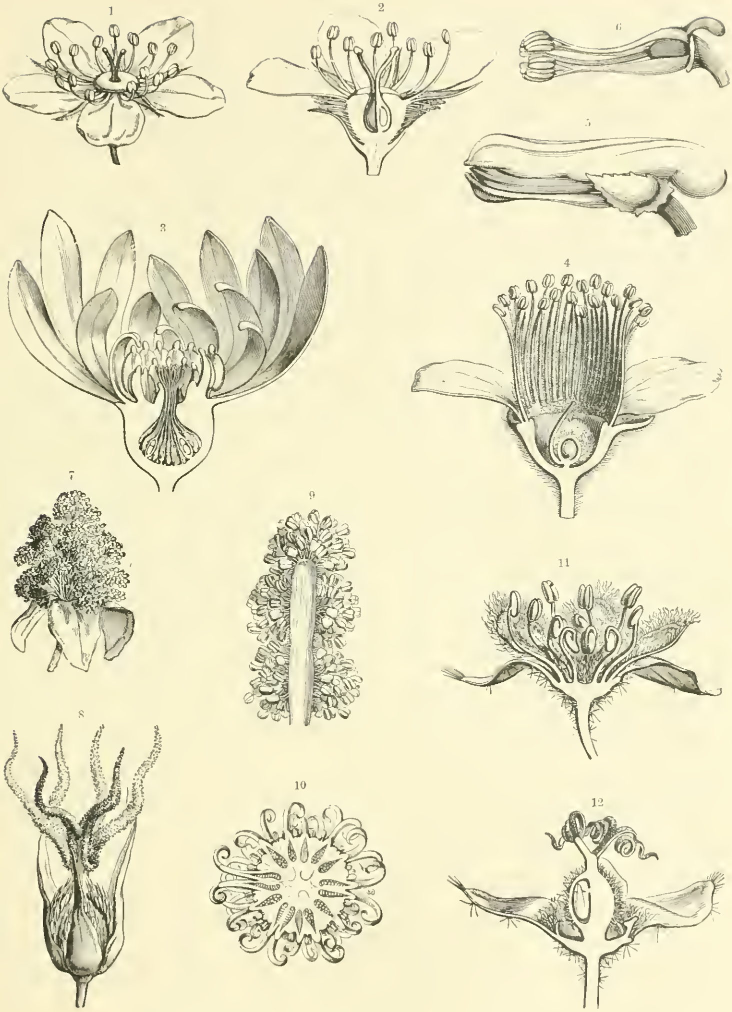


Fig. 285.—Types of the 11th, 12th, 17th, and 21st classes of the Linnean System.

[1], [2] *Agrimonia Eupatoria*, whole flower and section of same. [3] *Calycanthus*, cut through longitudinally. [4] *Chrysobalanus*, longitudinal section of flower. [5] *Fumaria officinalis*, whole flower. [6] The same flower after the removal of the petals. [7] Staminate flower of *Ricinus communis*. [8] Pistillate flower of *Ricinus communis*. [9] Staminate flower of *Liquidambar*. [10] Pistillate flower of *Liquidambar*. [11] Staminate flower of *Croton*. [12] Pistillate flower of *Croton*, both halved. All the figures somewhat enlarged.

stamens and pistil, and so might also be mistaken for hermaphrodite flowers, but closer examination shows that their ovaries do not develop sufficiently to produce fertile seeds. The ovules, and usually the stigmas as well, do not mature, but the pollen in the anthers attains its full power. (3) True pistillate flowers. In these only fertile ovaries are developed, and there is no trace of stamens. (4) True staminate flowers, the counterpart of the third group. They contain stamens whose anthers hold ripe pollen, but their ovaries are quite suppressed.

To the four types of unisexual flowers we shall apply short descriptive names, at once rendering the character of the flower apparent, and saving much needless iteration and confusion. (1) *Pseudo-hermaphrodite female flowers* are the pistillate flowers which appear to be hermaphrodite, similarly (2) *Pseudo-hermaphrodite male flowers* are the staminal flowers which, from the presence of reduced pistils, appear to be hermaphrodite. (3) True *pistillate flowers,* and (4) True *staminate flowers.*

Next to the unisexual come the neuter (sterile) flowers, in which the ovaries and stamens are either altogether absent, the flower consisting merely of petals and sepals, or the sexual organs if present are quite rudimentary and hidden away in the centre of the flower.

The kinds of flower enumerated here are connected together by numerous transitional forms. In the hermaphrodite flowers of the Knawel (*Scleranthus*) two or three of the four stamens are often sterile; they occupy their right position, but their anthers are shrivelled and contain no ripe pollen, only one or two of the stamens being properly developed. Of the eight stamens of the well-known garden-plant *Clarkea pulchella* only the four which alternate with the petals form fertile pollen, while the anthers of the other four are abortive. Sometimes five, six, seven, or even all the anthers are sterile. The Chickweed (*Stellaria media*) has ten stamens arranged in two whorls of five, but it rarely happens that all the anthers produce fertile pollen. Usually those of the five inner and often of a pair of the outer whorl are shrivelled and have no pollen. These instances evidently form good links between the true hermaphrodite and the pseudo-hermaphrodite flowers. The flower-heads of the Burnet (*Poterium polygamum*) consist of pistillate, staminate, and truly hermaphrodite flowers. In the staminate flowers sixteen stamens are formed; the hermaphrodite flowers may contain eight, seven, six, or gradually decreasing numbers down to only one. The other stamens are not even formed, not the slightest trace of them can be found. These flowers may be regarded as connecting the truly hermaphrodite with the pistillate flowers, for if the suppression of stamens be supposed to go still further, so that the last stamen has disappeared, then the flower is no longer hermaphrodite, but has become a true pistillate flower.

The gradations in the class of pseudo-hermaphrodite, pistillate, and staminate flowers are also very varied. The Fuller's Thistle (*Cirsium*), the Flowering Ash (*Fraxinus Ornus*), the Asparagus (*Asparagus officinalis*), the Date-plum (*Diospyros Lotus*), the Vine (*Vitis vinifera*), many Scabiouses, Saxifrages, Valerians, &c., all develop imperfect flowers, which are liable to be mistaken at first sight for truly hermaphrodite. They have plain well-developed ovaries, and stamens in whose anthers pollen-grains are formed in greater or less numbers; but experiments with this pollen have shown that when deposited on the stigma it emits no pollen-tubes, and consequently the flowers are not in reality truly hermaphrodite, but only apparently so. This is the case in some of the flowers in the panicle of the Horse Chestnuts (*Æsculus* and *Pavia*), in some species of Dock (*Rumex alpinus*, *obtusifolius*, &c.), and in some of the flowers in the centre of the heads of the Colt's-foot, Marigold, and Butter-bur (*Tussilago*, *Calendula*, *Petasites*). They appear hermaphrodite although the ovaries never form fruits with fertile seeds, because their stigmas are not capable of inciting the emission of pollen-tubes in the ripe pollen deposited on them. Again, there are many plants where either the ovaries or the stamens are so reduced that they can only be discovered by careful searching. Some examples of the red Campion (*Lychnis diurna*) have flowers with well-developed ovaries and stigmas, which are capable of fertilization, while their stamens are extremely minute, consisting of triangular bodies scarcely 1 mm. long, which bear a small polished head destitute of pollen instead of an anther. Other plants of this same Campion bear flowers with ten stamens whose long ribbon-like filaments are surmounted by large anthers with fertile pollen, but instead of the ovary there is only a minute knob with two points indicating the stigma. The same thing occurs in the flowers of some Valerians (*Valeriana dioica*, *simplicifolia*, &c.). The racemes of the Sycamore (*Acer Pseudo-platanus*) exhibit every imaginable gradation from pseudo-hermaphrodite male flowers, with comparatively large ovaries, to those in which the ovaries are reduced or altogether absent. I have mentioned these instances, to which many others might be added, to show that there is no lack of transitional forms between pseudo-hermaphrodite and truly pistillate and staminate flowers; and again, in plants with neuter flowers, especially in many species of the Grape-Hyacinth (*Muscari*), we have gradations from truly-hermaphrodite to neuter flowers. The remarkable structures known as gall-flowers (*cf.* pp. 159, 160) may also be mentioned here. They represent neuter flowers, and occasionally undoubted links are found between them and true pistillate flowers. In spite of these transitional forms, which to some extent break down the limits between the various kinds of flower, it is advisable to retain the names already used for the separate forms, since otherwise it would be impossible to give a general account of the arrangement of the sexes in Phanerogams.

It has been stated above that botanists were formerly content with dividing plants according to their sex into those with hermaphrodite, monœcious, diœcious, and polygamous flowers (*cf.* p. 291). This classification, however, is no longer adequate to the present standpoint of our knowledge. I will now attempt to give an approximate account of the extremely complex conditions which must be considered in this matter, but will keep to the old divisions as far as possible in so doing.

We may place in the first group those plants whose species develop true hermaphrodite flowers exclusively. Although this group is not so comprehensive as it was thought to be in the time of Linnæus, it is nevertheless the most important, and includes more than a third of all the Phanerogams. The *Alpinia*, Lilac, Cornel, *Gagea*, Spurge Laurel, Flowering Rush, *Phytolacca*, Agrimony, Lime, Anemone, Bitter-cress, Baobab, and *Melaleuca*, all figured on pp. 289, 292, 293, may be mentioned as examples.

Close to these comes a second group of species which bear pseudo-hermaphrodite female flowers as well as truly hermaphrodite flowers, as, for example, *Oxyria digyna* and *Geranium lucidum*.

The third group includes those species whose individuals develop both true hermaphrodite flowers and those which appear to be so, but are really pseudo-hermaphrodite male flowers. Though instances of the second group are rare, the third comprises hundreds of species from widely-different families. Special instances are furnished by the North American Shrubby Trefoil (*Ptelea trifoliata*), the common Bistort (*Polygonum Bistorta*), the Horse-Chestnuts (*Æsculus, Pavia*), some Aralias (e.g. *Aralia nudicaulis*), several species of Bed-straw and Woodruff (e.g. *Galium Cruciata, Asperula taurina*), and many Umbelliferæ. In the last-named the arrangement and distribution of the two kinds of flowers is quite determinate for each genus, and has the closest connection with the processes of pollen-transfer. In *Anthriscus* the umbellate heads of the central umbel contain for the most part true hermaphrodite flowers surrounded by a few pseudo-hermaphrodite male flowers. The heads of the lateral umbels, however, are composed entirely of these staminate flowers. In *Caucalis* the central umbellate heads consist exclusively of pseudo-hermaphrodite male flowers, while the other heads are formed of 2 true hermaphrodite flowers and 4–7 pseudo-hermaphrodite male flowers. In *Astrantia* the large central umbels contain 12 hermaphrodite flowers surrounded by a few pseudo-hermaphrodite male flowers, but the lateral, smaller umbels contain the latter only. *Athamanta cretensis, Chærophyllum aromaticum* and *Meum Mutellina* have in all their umbels a central hermaphrodite flower surrounded by staminate flowers (*i.e.* male pseudo-hermaphrodites), and these in turn are surrounded by true hermaphrodite flowers. All the umbels of *Chærophyllum Cicutaria* and *Laserpitium latifolium* contain short-stalked pseudo-hermaphrodite male flowers surrounded by long-stalked truly hermaphrodite flowers. In the centre of all the umbels of *Turgenia latifolia* are 6–9 pseudo-hermaphrodite flowers which do not radiate, and 5–8 true hermaphrodite flowers, ray-like on the circumference; whilst in *Sanicula europæa* there are three central hermaphrodite flowers in each umbel surrounded by 8–10 pseudo-hermaphrodite male flowers.

In the fourth group each plant bears both truly hemaphrodite and truly pistillate flowers. A large number of Composites come under this heading, of which the Asters may be taken as a type (*Aster, Bellidiastrum, Stenactis, Solidago, Bupthalmum, Inula, Arnica, Doronicum*, &c.). The tubular florets of the disc are truly hermaphrodite in each capitulum, while the tongue-shaped ray-florets are truly pistillate. This division of the sexes also occurs in other Compositæ, of which the genera *Homogyne* and *Helichrysum* may be taken as typical, where the ray-florets are not tongue-shaped but threadlike. This arrangement is rarely met with except in these Composites. Strangely enough, it occurs in a species of Gladiolus (*Gladiolus segetum*).

The fifth group is made up of species where every plant bears both hermaphrodite and true staminate flowers. For examples we have the so-called White Hellebore (*Veratrum*), the Crown Imperial (*Fritillaria imperialis*), the Snake-root (*Calla palustris*), and numerous Grasses belonging to the genera *Andropogon*, *Arrhenatherum*, *Hierochloa*, *Holcus*, and *Pollinia*.

A sixth group comprises those species in which every plant bears both true pistillate and pseudo-hermaphrodite male flowers, but none that are truly hermaphrodite. In this group are placed the Marigold (*Calendula*), the Colt's-foot (*Tussilago*), and *Micropus*. Here tubular staminate flowers (which are really pseudo-hermaphrodite) occupy the centre of the capitulum, and true pistillate flowers, either tongue-shaped or filiform, occur at the circumference. The Edelweiss (*Gnaphalium Leontopodium*) and the Butter-bur (*Petasites*) also belong to this group. In the two last-named plants, however, the arrangement in the single capitula is of a peculiar kind differing from that in the other Composites mentioned. There are three kinds of individuals of Edelweiss. In one the central head of the whole inflorescence contains only pseudo-hermaphrodite male flowers, whilst in the second form the central capitulum is again formed entirely of pseudo-hermaphrodite male flowers, but in the other capitula these are surrounded by true pistillate flowers. In the third form all the capitula have pseudo-hermaphrodite male flowers surrounded by true pistillate flowers. In the Butter-bur (*Petasites*) all the capitula have pseudo-hermaphrodite male flowers in the centre, and true pistillate flowers around the circumference, but strangely enough the number of these varies from plant to plant. In some plants the pseudo-hermaphrodite male flowers are very numerous, and the capitula contain but few true pistillate flowers and *vice versâ*. These two kinds of plants differ very much in appearance, and the Butter-bur might therefore be easily mistaken for a diœcious plant.

The seventh group includes all those species in which each plant develops both true staminate and true pistillate flowers, species which have been previously termed monœcious. Examples of this large group are: Oak (*Quercus*; see fig. 286), Hazel (*Corylus*; see fig. 235, p. 147), Alder (*Alnus*; see fig. 228, p. 135), Walnut (*Juglans*; see fig. 184, vol. i. p. 742), Pine (*Pinus*; see fig. 233, p. 144), many Urticaceæ (*Urtica urens*, *Pachysandra*), numerous Aroids (*Arum*, *Ariopsis*, *Arisema*, *Richardia*, &c.), many Palms, a number of marsh and water plants (*Myriophyllum*, *Sagittaria*, *Sparganium*, *Typha*, *Zannichellia*), some Grasses (*Heteropogon*, *Zea Mays*), and, especially, many Euphorbiaceæ and Cucurbitaceæ.

Species belonging to the eighth group have three kinds of flower side by side on the same plant, *i.e.* pseudo-hermaphrodite male and pseudo-hermaphrodite female flowers and true hermaphrodite flowers. Examples are furnished by various Acers (*Acer Pseudo-platanus* and *platanoides*), Sumachs (e.g. *Rhus Cotinus* and *Toxi-*

codendron), Laurels (e.g. *Laurus nobilis* and *Sassafras*), many Docks (e.g. *Rumex alpinus* and *obtusifolius*), the Wall Pellitory (*Parietaria*), and also some Saxifrages (e.g. *Saxifraga controversa* and *tridactylites*).

The ninth group consists of species whose individuals each bear true hermaphrodite flowers along with true pistillate and true staminate flowers. The Ash (*Fraxinus excelsior*; see fig. 230, p. 138) is an example of this group.

Now come the groups whose species contain two or three kinds of flowers *distributed on two or several plants.*

Species belonging to the tenth group bear true hermaphrodite flowers on one plant and pseudo-hermaphrodite female flowers on another. Examples of this are: numerous Valerians (e.g. *Valeriana montana, Saliunca, supina*), some Dipsaceæ (e.g. *Scabiosa lucida, Knautia arvensis*), many Saxifrages (e.g. *Saxifraga aquatica*), the cultivated Vine (*Vitis vinifera*), many Caryophyllaceæ (e.g. *Dianthus glacialis* and *prolifer, Lychnis Viscaria, Silene noctiflora*), and, especially, very many Labiatæ (e.g. *Calamintha, Glechoma, Marrubium, Mentha, Origanum, Prunella, Thymus*).

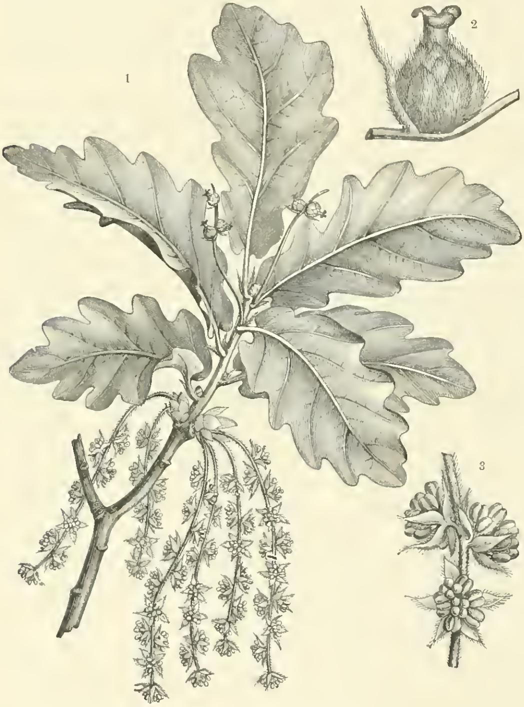


Fig. 286.—Type of a monœcious plant.

1 Oak (*Quercus pedunculata*); pistillate flowers on the upper part of the twig, staminate flowers (in pendent catkins) below. 2 A single pistillate flower of the same plant. 3 Three staminate flowers of the same plant. 1 nat. size; 2 and 3 × 4.

In the eleventh group we place those plants which develop true hermaphrodite flowers on one plant and pseudo-hermaphrodite male flowers on another, as, for example, numerous Ranunculaceæ (e.g. *Ranunculus baldensis, Pulsatilla alpina, vernalis, Ranunculus alpestris, glacialis*), many Rosaceæ (e.g. *Dryas octopetala, Geum montanum* and *reptans*), and many species of Vine (e.g. *Vitis sylvestris, macrocirrha*).

The twelfth group comprises those species which bear pseudo-hermaphrodite female flowers on one plant and pseudo-hermaphrodite male flowers on another. This is observed in species of Buckthorn of the section Curvispina (*Rhamnus cathartica, saxatilis, tinctoria*), in various Caryophyllaceæ (e.g. *Lychnis diurna* and *vespertina*), in Asparagus (*Asparagus officinalis*), the Rose-root (*Rhodiola rosea*), the Mountain Currant (*Ribes alpinum*), and the Fuller's Thistle (*Cirsium*).

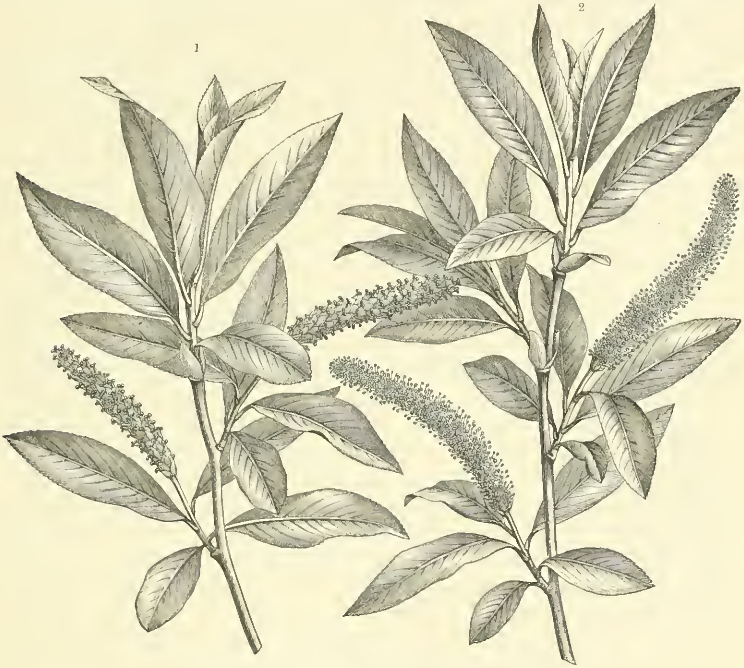


Fig. 287.—Type of a diœcious plant: Crack Willow (*Salix fragilis*).

[1] Twig with pistillate catkins. [2] Twig with staminate catkins. Natural size.

The Mountain Cudweed (*Gnaphalium dioicum*) and the closely allied species of the same genus, *Gnaphalium alpinum* and *carpaticum*, also belong to this group.

The thirteenth group contains numerous species all bearing true pistillate flowers on one plant and true staminate flowers on another; they were termed *diœcious* by Linnæus. Examples are: *Ephedra*, Cycads, Juniper, Yew, and Ginkgo (*Juniperus, Taxus, Ginkgo*), numerous Sedges (e.g. *Carex Davalliana, dioica*), *Vallisneria* (see fig. 155, vol. i. p. 667), Hemp and Hop (*Cannabis, Humulus*), the Paper Mulberry (*Broussonetia papyrifera*; see fig. 229, p. 137), Dog's Mercury

(*Mercurialis*), some Docks (*Rumex Acetosa, Acetosella*), Sea Buckthorn (*Hippophae*), Poplar (*Populus*), and the Willows, one of which is figured on last page.

The fourteenth group consists of species which bear true hermaphrodite flowers on one plant and pseudo-hermaphrodite female flowers on another, and pseudo-hermaphrodite male flowers on a third plant. Caryophyllaceous plants afford many examples of this group, viz. *Saponaria ocymoides, Silene acaulis, nutans, Otites* and *Saxifraga*. This arrangement is less often met with in Gentians, as, for example, in *Gentiana ciliata*.

A fifteenth group may be added, in which the species have their three kinds of flowers distributed in four ways on different plants, so that they can be divided into four varieties. *Spiræa Aruncus* is typical of this. It produces true hermaphrodite flowers and pseudo-hermaphrodite male and female flowers. The three kinds of flowers are arranged thus: (1) some plants bear only pseudo-hermaphrodite female flowers, (2) others only pseudo-hermaphrodite male flowers, (3) some bear both hermaphrodite flowers and pseudo-hermaphrodite male flowers, and (4) in addition there are yet other plants whose flowers are all hermaphrodite.

To complete this summary it should be mentioned that some species exhibit deviations from their usual distribution of the sexes, although this is not often the case. For instance, plants of the diœcious Nettle (*Urtica dioica*) sometimes occur with both true pistillate and staminate flowers on the same individual. The same thing is occasionally seen in Willows. Most of the plants of the Wild Basil (*Clinopodium vulgare*) in a given locality bear hermaphrodite flowers, but from a few of the flowers on some plants anthers are either partially or wholly absent. Staminate plants of *Vitis cordata* were grown in the Vienna Botanical Gardens and only developed staminate flowers for many years, but occasionally true hermaphrodite flowers appeared as well. Single staminate flowers have been repeatedly observed on the pistillate plants of the diœcious Dog's Mercury (*Mercurialis annua*), and in *Lychnis diurna* and *vespertina* true staminate flowers and isolated hermaphrodite flowers are sometimes found together. Single hermaphrodite flowers occur here and there in the inflorescences of the Castor-oil plant (*Ricinus communis*) among the true pistillate and staminate flowers, and on many plants of *Saponaria ocymoides* true hermaphrodite and pseudo-hermaphrodite female flowers have been seen together with pseudo-hermaphrodite male flowers.

In the light of these results of recent investigation it is evident that the theory expressed in the Linnean System, viz. that the great majority of Phanerogams bear only hermaphrodite flowers, is not confirmed, and that the view held by Linnæus as to the completeness and importance of this type of flower breaks down with it.

But since it is now established that the separation of the sexes in the Vegetable Kingdom is such a widespread phenomenon, it must offer some advantage, and this advantage can only lie in connection with cross-fertilization. By *cross-fertilization* in Phanerogams we mean here the transference of pollen-cells from one flower to the stigma of another which contains the female sexual cells in its ovary; and we may distinguish between crossing in plants of the *same* and of *different* species. In the former case the pollen of one flower is deposited on the stigma of another flower belonging to a plant of the *same* species; in the latter case the pollen is deposited on the stigma of a flower which is *not of the same* species. Obviously in the latter process, which is also termed *hybridization*, the two flowers are some distance apart. Of the former process there are two varieties, viz. *Geitonogamy* (from γείτων, a neighbour, and γάμος, marriage), when the two flowers are immediate neighbours, growing upon the same plant, and *Xenogamy* (from ξένος, a stranger, and γάμος, marriage), when they are on different plants of the same species.

Although the distribution of the sexes on different plants or in different flowers of the same plant has been indicated as advantageous, even as a condition for the occurrence of cross-fertilization, it must not be supposed that it is the only contrivance for ensuring hybridization, xenogamy, or geitonogamy. It is beyond question that the same result is obtained in true hermaphrodite flowers, *i.e.* that plants whose flowers all contain fertile pollen-grains and ovaries which are capable of development can cross with one another. Of course special arrangements are necessary for this, and the more important of them will be mentioned in the following pages and illustrated by a few examples. In some instances cross-fertilization is unavoidable from the mutual arrangement and position of the two kinds of sexual organs which occur together in a true hermaphrodite flower. If during the whole time of flowering the stigma assumes such a position as to be brushed by an insect which is visiting the flower, but at the same time is so placed that it cannot receive the pollen from the anthers immediately surrounding it, it may be safely assumed that it is adapted to cross-fertilization. This is the case, for example, in the White Lily (*Lilium album*), Day Lily (*Hemerocallis flava* and *fulva*), *Anthericum*, and numerous bulbous plants of the Cape (*Amaryllis*, *Albuca*, &c.) The entrance to these flowers is directed laterally, and the style projects so far beyond the anthers with their sticky pollen that its stigma never receives any of it. On the other hand, when the projecting style is used as a resting-place by flying animals which come laden with pollen from another flower, it is unavoidable that foreign pollen should be deposited on the stigma, and so a crossing results. The same is true of various Boraginaceæ (e.g. *Echium*), Scrophulariaceæ (e.g. *Pæderota Ageria*), Bindweeds (e.g. *Convolvulus sepium*, *sylvaticus*, *lucanus*), Caprifoliaceæ (e.g. *Linnæa borealis*), Rhododendrons (e.g. *Rhododendron Chamæcistus*), and Cactaceæ (e.g. *Mammillaria*, *Echinocactus*). Many flowers whose entrance is directed upwards (e.g. *Lilium bulbiferum*, *Glaucium luteum*, *Gentiana Bavarica*, *nivalis*, *verna*) show the same condition of anthers and stigmas. In the flowers of the Mezereon (*Daphne Mezereum*) the stigma is not beyond and above the anthers, as in the plants just mentioned, but it forms the termination of the ovary at the base of the perianth-tube, whilst the anthers are situated in the upper part of the tube. Some pollen may occasionally fall from the anthers on to the stigmas in erect flowers, especially when they shrivel up as the blossom fades, but the majority of Mezereon flowers stand out horizontally from the branches, and in these it is hardly possible for the adhesive pollen to reach the stigmas unaided, although the anthers and stigma are not more than 2 mm. apart. Mezereon flowers are visited so industriously by bees, however, that most of the stigmas are pollinated by strange pollen, and thus manifold crossings are obtained. In the majority of Orchids, too, the pollen is only brought from its hiding-place by insects which hardly ever deposit it on the adjacent stigma, but as a rule transfer it to the stigma of another flower.

Heterostyled plants present a peculiar condition. Many Gentianaceæ (e.g. *Menyanthes trifoliata*, *Gentiana Rhætica* and *Germanica*), the various species of Bastard Toadflax (*Thesium*), numerous Primulaceæ (e.g. *Androsace*, *Aretia*, *Gregoria*, *Hottonia*, *Primula*, see figs. 288 [1] and 288 [2]) as well as many Boraginaceæ (e.g. *Myosotis*, *Mertensia*, *Pulmonaria*; see figs. 288 [3] and 288 [4]) and members of other groups, bear flowers with relatively short styles on one plant, the anthers being above the stigma, while, on another plant of the same species, the flowers have all relatively long styles, and the anthers are inserted below the stigma. At the opening of the flowers the stigmas cannot receive pollen unaided either from the anthers above or from those below them. But an insect, which, by inserting its proboscis into a short-styled flower, has brushed against the anthers at the mouth of the corolla-tube, and thus loaded itself with pollen, will deposit this exactly on the stigma of a long-styled flower, should it enter one, since the stigma is just at the same level in the second flower as the circle of anthers in the first-visited, short-styled form. In the same way it is hardly necessary to say that the pollen, which has adhered to the proboscis of a honey-sucking insect half-way up the corolla-tube of a long-styled flower, will be deposited on the stigma which reaches the same level in a

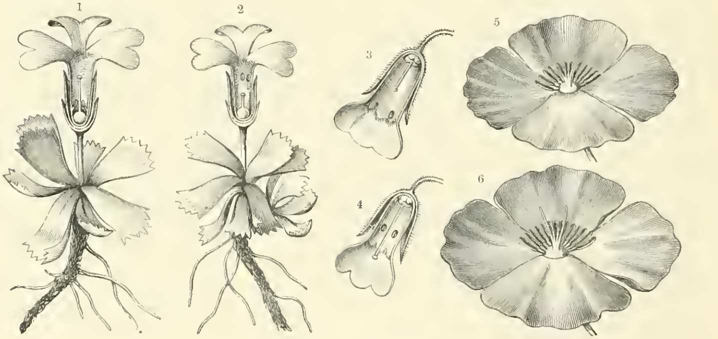


Fig. 288.—Heterostyled flowers.

[1] Plant of *Primula minima* with a long-styled flower. [2] Plant of the same species with a short-styled flower. [3] Short-styled flower of *Pulmonaria officinalis*. [4] Long-styled flower of *Pulmonaria officinalis*. [5] Short-styled flower of *Eschscholtzia Californica*. [6] Long-styled flower of the same plant. All nat. size.

short-styled flower. I shall return to the subject of heterostyly in the next chapter, and will merely say here that there are also plants whose anthers and stigmas present three kinds of arrangement. For example, in the Purple Loosestrife (*Lythrum Salicaria*) the flowers on one plant will have long styles, on another medium styles, and short styles on a third plant; the two whorls of stamens in plants with long-styled flowers are below the stigma; in the medium-styled flowers, one whorl of anthers is above, and the other below the stigma; whilst in the short-styled flowers both whorls of anthers are above the stigma. We should also briefly state here that the *Eschscholtzia*, which usually possesses four styles (figs. 288[5] and 288[6]), develops styles of unequal length in its flowers; in some flowers, which are distinguished by their larger circumference, there are two longer and two shorter. The longer styles receive the pollen from other flowers, and are adapted to cross-fertilization, while the shorter styles are pollinated by the anthers standing close beside them (fig. 288[6]). There are also smaller flowers containing four styles which are all so short that they do not project above the pollen-producing anthers (fig. 288[5]). We can only briefly touch upon the remarkable Ranunculaceæ and Rosaceæ (*Anemone baldensis, Pulsatilla alpina, vernalis, Ranunculus alpestris, glacialis, Geum montanum, reptans,* &c.) which develop pseudo-hermaphrodite male flowers, as well as two kinds of hermaphrodite flowers, those with large ovary and few short stamens, and those with small ovary and numerous long stamens; but it may be stated that the former are adapted to crossing, and the latter to autogamy.

Another contrivance for promoting cross-fertilization is the interchange of position of anthers and stigmas. Although this has been repeatedly mentioned already (see pp. 250 and 276), it must again be described, since it represents one of the most important contrivances for the crossing of hermaphrodite flowers, and can only be completely understood when regarded from this point of view. The change of position consists essentially in this; the place occupied for some time by the ripe stigma is assumed later by the pollen-laden anthers, and *vice versâ*. Since this position is directly in the path traversed by the honey-sucking insect as it enters, the pollen is brushed on to the stigmas in one flower and collected from the anthers in another—a condition necessarily leading to cross-fertilization. This change of position is brought about by spontaneous movements in the anther-filaments, or by similar changes of direction in the styles. It may even happen that both the stamen-filaments and the styles of the same flower alter their position and actually exchange places. We may distinguish no less than *ten* different varieties of this change of position.

In one group of plants, of which the Dwarf Leek (*Allium Chamæmoly*) may be taken as an example, the ripe stigma is seen in the middle of the newly-opened flower, while the anthers are pressed back against the perianth-leaves. Later, as the anthers open and expose their pollen, they pass towards the centre by reason of the peculiar movement of their filaments till they come close to the stigma and form a yellow ball. This is necessarily touched by an insect as it enters the flower, although previously only the stigma would have been brushed in the same position.

In a second group, to which belong many Gentians (*Gentiana asclepiadea, ciliata, Pneumonanthe*), most Malvaceæ (*Abutilon*, *Malva*), the numerous species of Monkshood (*Aconitum*), *Funkia*, and the Red Valerian (*Centranthus*), the pollen in a young flower is exposed close to the path of the honey-seeking insect; sometimes only from a single anther (as in *Centranthus*, figs. 289 ¹˒ ²˒ ³), sometimes from five or six, or from quite a number united together in one bundle (Malvaceæ). The stigmas are at first hidden behind, *i.e.* below the anthers; later on the anther-filaments bend back in a semicircle, and the stigmas are exposed. When only a single stigma is present (hitherto hidden behind the anther as in *Centranthus*) of course only one can be displayed (see figs. 289 ² and 289 ³). When an insect comes for honey it strikes against the exposed stigmas, just as it did previously against the anthers.

The third group contains species of *Gladiolus, Acanthus,* Penstemon, and Sage (*Salvia*; see fig. 271, p. 262). The styles and stigmas of the horizontally-directed flowers of these plants lie close against the roof-like portion of the corolla above the anthers, but later the style bends down until the stigma lies just in the path which leads to the honey, so that insects passing this way (laden with pollen from the younger flowers) deposit it in older ones, so producing cross-fertilization.

In the fourth group, to which belong the genera *Allionia* and *Phalangium*, the stigma at the commencement of flowering is at the end of the projecting style in front of the anthers, and insects flying to the flowers are obliged to brush against this stigma. Afterwards the style bends sideways through an angle of 80–90°, so that the stigma is removed from the road leading to the honey. Now, when insects fly to the flower they come in contact with the pollen-covered anthers only.

In flowers of the fifth group, of which the Germander (*Teucrium*; see figs. 289 ⁴˒ ⁵ ⁶) is a type, the change of position resembles that of *Centranthus* in that the thread-like anther-filaments are placed at the aperture of the flower, so that insects strike against the anthers as they enter. Afterwards the stamens bend up, and the anthers are removed from the path, whilst concurrently the stigmas are exposed. But there is this important difference—in the Germander the style as well as the stamens alters its direction and position and bends downwards like a bow till the stigmas come to lie in exactly the same position as was previously occupied by the anthers.

In the flowers of the sixth group, typical examples of which are furnished by the sweet Basil (*Ocymum Basilicum*) and the well-known climber, *Cobæa scandens,* the same kind of change of position occurs as in the Germander; but the stamen-filaments bend down instead of up, and the style upwards instead of downwards. At the beginning of flowering the anthers intercept the passage to the honey at the base of the flower, but later on they sink downwards, while the style arches up, bringing the stigma to the identical place previously occupied by the anthers.

The remarkable change of position of stigmas and anthers in plants of the seventh group as shown by the Nightshade (*Atropa*), *Scopolia*, Henbane (*Hyoscyamus*) and the Mandrake (*Mandragora*) has been already described on p. 278 and illustrated in figs. 279 [8] and 279 [9]. In young blossoms the stigma stands in the middle of the flowers, and the anthers lie against the walls of the corolla: in older flowers the anthers stand in the middle, and the style becomes pressed against the corolla.

The shrubby species of Honeysuckle (*Lonicera alpigena, nigra*, and *Xylosteum*), and the genus *Scrophularia* may be taken as examples of the eighth group. Their flowers are horizontally placed. At first the straight style rises out of the centre of the flower, and the stigma is held directly in the path leading to the honey. The anthers are above the stigma in *Lonicera*, but in *Scrophularia* they are hidden at the end of their arched filaments in the cavity of the pitcher-shaped corolla. Later on the stigma is moved out of the path by the downward curvature or sharp bending of the style, the anthers assuming the position occupied by the stigma by means of a corresponding straightening and alteration of direction of their filaments.

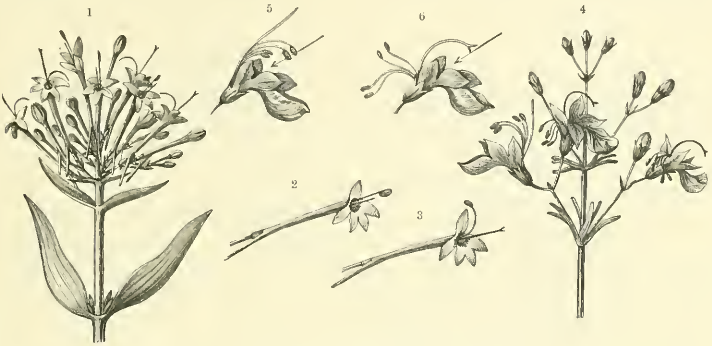


Fig. 289.—Change of Position of Anthers and Stigmas.

[1] Inflorescence of the Red Valerian (*Centranthus ruber*). [2] A single flower of the Red Valerian shortly after opening. [3] The same flower at a later stage. [4] Inflorescence of *Teucrium orientale*. [5] Single flower of the same plant shortly after opening. [6] The same flower at a later stage. [1] and [4] nat. size; [2], [3], [5], and [6] somewhat magnified.

The Hellebore (*Helleborus*), a type of the ninth group, has comparatively large flowers with abundant honey. The honey is not in the centre of the flower, as in the instances quoted above, but is secreted in cornet-shaped receptacles outside the ring of stamens. Accordingly the honey-sucking insects do not go to the centre of the flower but to the circumference, and this explains why the stigmas and anthers, which are to be brushed by the insects, are arranged in a corresponding circle. When the flower opens the styles radiate outwards, and are bent, so that the stigmas stand over the honey receptacles. The anthers are crowded together in the middle of the flower, and are not touched by the insect as it enters. Afterwards the styles straighten and move towards the centre of the flower while the stamen-filaments elongate, and thus assume a position overhanging the honey receptacles, where they are inevitably brushed by insects.

For the tenth group we may select the Rue (*Ruta*; see fig. 290) as an example. The flower contains ten anthers supported by stiff filaments, arranged in the form of a star. First, one of these filaments bends up and places its anther in the middle of the flower, just in the way to the fleshy ring which secretes nectar at the base of the pistil: it remains there about a day, and then bends back and resumes its former position. While the first stamen is bending back, a second rises up and undergoes the same movements. And so it goes on until the ten anthers have all stood in the centre of the flower in turn and discharged their pollen there. When, finally, the last stamen has bent back again, the stigma, which has meanwhile matured, is seen in the centre of the flower where the anthers have successively shed their pollen.

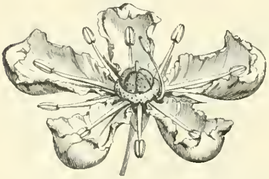


Fig. 290.—Flower of the Rue (*Ruta graveolens*) × 3. (After Baillon.)

A process which is closely connected with the interchange of position of anthers and stigmas, in bringing about cross-fertilization between hermaphrodite flowers, is the separation and subsequent falling away of the stigmas when the surrounding anthers begin to dehisce. We may take one of the Urticaceæ, the Wall Pellitory (*Parietaria*; see figs. 291 [2, 3, 4]), as a type of this. The stigma is always developed before the flowers open in this plant, and at the commencement of the flowering period it may be seen projecting like a dusting-brush from the green flower-bud (fig. 291 [3]). The curved anther-filaments are at this time coiled like watch-springs and covered over by the as yet unopened floral-leaves. Before these filaments jerk up and scatter their pollen the stigma withers and shrivels up and the style becomes detached from the ovary. It falls off with the dried-up stigma, so that, when the pollen is liberated from the anthers, the ovary is terminated merely by a small stump which is really the withered remnant of the fallen style (fig. 291 [4]).

The falling of the anthers and stamens at the time when the adjoining stigmas become mature is of much more frequent occurrence than the detachment and falling of the stigmas before the pollen is shed. In the flowers of Balsams (*Impatiens glandulosa, Nolitangere, tricornis,* &c.) the anthers are united into a kind of cap which arches over the stigma. As soon as the flower has opened and become accessible to flying insects, the anthers dehisce and only the cap which they form can be seen at the entrance to the flower. Later, the filaments of the anthers become detached, and the anther-cap falls out of the flower; only the stigma, which has meanwhile matured, is now visible in the middle of the flower. The large-flowered species of Crane's-bill (e.g. *Geranium argenteum, pratense, sylvaticum*; see fig. 291 [1]) have a similar arrangement. Two of the anthers which have hitherto been covered by the petals dehisce almost simultaneously with the opening of the flower; the others then open in a certain order and expose their pollen in turn. The stigmas in the centre of the flower are still folded together: as soon as they begin to separate the anthers fall away from their filaments, and the five mature outspread stigmas are surrounded only by the needle-shaped filaments minus their anthers (fig. 291 [1], the left-hand flower). The same thing happens in some Saxifrages, of which *Saxifraga rotundifolia* (fig. 292) will serve as a type. After the petals have unfolded, a peculiar action on the part of the stamens is to be observed for several days. Each anther as it dehisces is raised up by its filament into an erect position (see fig. 292 [2]), but remains in this position only for a short time; it bends down again the next day or the next but one, resuming its original position. The anther falls off, or if it remains as a shrivelled mass on the top of the filament it has by this time lost all its pollen. All the stamens in succession undergo this rising and sinking. Not until all the pollen has disappeared do the two short styles, which up till now have been folded together like the two ends of a pair of tongs (fig. 292 [2]), separate from one another, and their stigmas become capable of pollination (fig. 292 [3]). The Grass of Parnassus (*Parnassia palustris*; see fig. 267 [4], p. 249) as well as many Caryophyllaceæ (e.g. *Alsine verna*, *Silene Saxifraga*), many Valerians (e.g. *Valeriana officinalis*) and Tulips (e.g. *Tulipa Didieri*) exhibit the same course of development, especially the falling away of the anthers. In Caryophyllaceæ it often happens that the antherless filaments bend down in a semicircle under the petals and become so hidden that the flower might at first sight be thought to be pistillate instead of truly hermaphrodite.

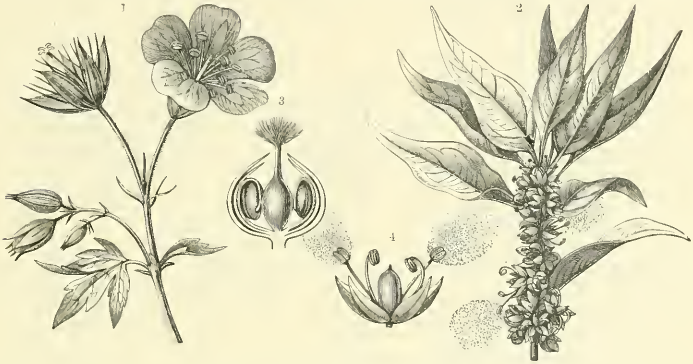


Fig. 291.—Completely dichogamous Flowers.

[1] *Geranium sylvaticum* with completely protandrous flowers. [2] *Parietaria officinalis* with completely protogynous flowers. [3] Single flowers of *Parietaria* with mature brush-shaped stigma and closed coiled-up stamens. [4] The same flower at a later stage of development; the stigma has fallen off, the filaments have straightened, and the anthers are flirting out their dusty pollen. [1] and [2] nat. size; [3] and [4] somewhat magnified.

The end gained by this shedding of the anthers in the Balsam, Saxifrage, Grass of Parnassus, Chickweed, Pink, and numerous other plants with hermaphrodite flowers, is also obtained in the following manner:—The anthers are covered over and hidden by the petals as soon as the neighbouring stigma begins to mature, so that they are no longer able to shed their pollen. The consequence is that the stigmas can only be pollinated with foreign pollen, which is of course the same thing as saying that only cross-fertilization can occur in these hermaphrodite flowers. In the hermaphrodite flowers of the Spiderworts (*Tradescantia crassula, Virginica,* &c.), the anthers dehisce a considerable time before the stigmas mature. When the flower first opens, therefore, pollen only can be removed. But as soon as the stigmas become capable of fertilization the stamens roll up in a spiral, and soon afterwards the perianth withers and forms a moist, pulpy mass, quite covering the anthers on their rolled-up filaments. The style still projects stiffly from the flower and the stigmas remain capable of fertilization the whole of the following day. Small flies and other insects with short probosces now visit these flowers to suck up the juice of the pulpy petals, and at the same time the stigma is pollinated with pollen which they have brought from distant flowers, it being impossible to obtain that of the neighbouring anthers. It is an odd fact that some of the flowers of a *Tradescantia* plant, all of which opened simultaneously in the morning, will be already closed the same evening, whilst others will remain open the whole of the following day. It would seem that in those flowers which remain open the succulent hairs of the staminal filaments are devoured by flies, thus is the pollen obtained which is to be taken to the stigmas of the flowers whose anthers are hidden under the pulpy perianth. A peculiar process is observed in the flowers of *Telephium Imperati,* a native of Southern Europe, belonging to the Caryophyllaceæ. Here the anthers open first, but, as soon as the stigmas mature, the anthers—even if they have not as yet discharged all their pollen—are covered over by the petals, so that only pollen from other younger flowers can reach the ripe stigmas.

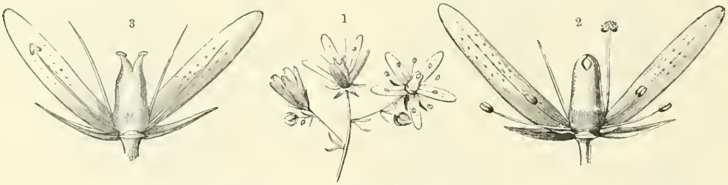


Fig. 292.—Dichogamy in *Saxifraga rotundifolia.*

[1] A portion of the inflorescence with flowers at different stages: that to the right still young, in the middle older. [2] Longitudinal section through a single flower with folded stigmas and one stamen shedding its pollen. Another stamen (to left of pistil) has lost its anther, and four others have anthers which have not yet dehisced. [3] The same flower at a later stage of development, with mature stigmas. [1] nat. size; [2] and [3] × 4-5.

By these contrivances the same result is obtained in hermaphrodite flowers as by the separation of the two kinds of sexual organs on different plants, or on different flowers of the same plant. In all cases it seems to be the separation of the two kinds of sexual organs within the limits of the same species which is aimed at. The separation of the two kinds of sexual organs by the non-simultaneous maturation of the pollen and of the stigmas in any one species is just as effective in promoting cross-fertilization as their separation by actual distance. In other words, separation in time is as efficient as separation in space; and these flowers, though structurally hermaphrodite (in that they contain both male and female organs), are —as the mechanism works out—unisexual (in that only one set of organs is mature at any given moment). This maturation of the sexual organs so that they are capable of fertilization at different times in the same plant, is termed *dichogamy* (δίχα, apart, and γάμος, marriage), and we may distinguish between *protogynous* and *protandrous dichogamy*. If the stigmas are able to receive pollen, retain it, and stimulate it to put out pollen-tubes at a time when the pollen in the same flower is still unripe and hidden in the anthers, this particular species is termed *protogynous* (from πρῶτος, first, and γύνή, a woman). But if the pollen is shed from the dehisced anthers, whilst the stigmas in the same flower are yet immature, *i.e.* not susceptible to pollination, then the species is said to be *protandrous* (πρῶτος, first, and ἀνήρ, a man). In the racemose inflorescence of the Willow-herb (*Epilobium angustifolium*), which is represented in fig. 293 [1], the upper flowers are seen to be still closed; a little lower are three flowers which have just opened, the middle one being visited by a

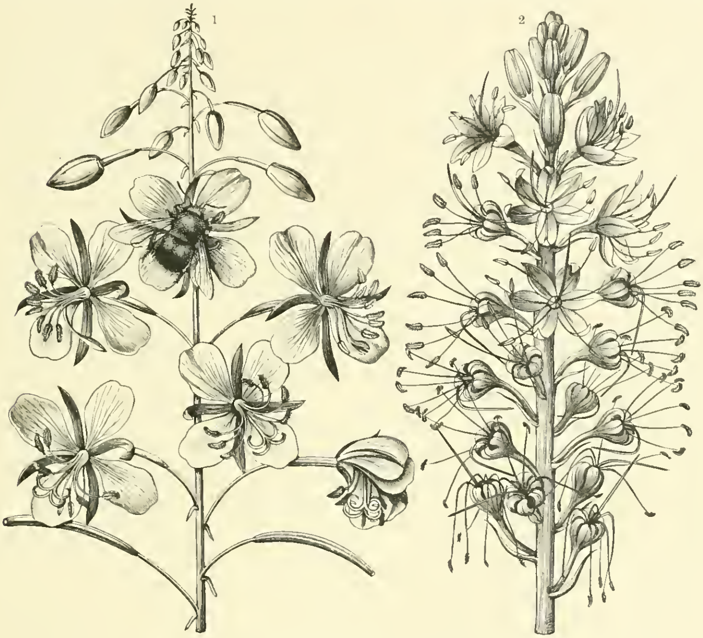


Fig. 293.—Incompletely dichogamous Flowers.

[1] *Epilobium angustifolium* with protandrous flowers. [2] *Eremurus Caucasicus* with protogynous flowers.

humble-bee, whilst lower still are flowers which have been open for two days. In the recently-opened flowers the anthers are covered with pollen, while the stigmas on the end of the downwardly-curved style are as yet immature and folded together into a club-like body. This plant is therefore protandrous. The inflorescence of *Eremurus Caucasicus*, belonging to the Liliaceæ, is figured beside it (293 [2]). Here, again, the youngest flowers are still in bud, those coming next below have just opened, whilst lower down still are the oldest flowers of all. In the newly-opened flowers the anthers are closed and no pollen is exposed, but the pointed stigma, terminating the upwardly-curved style, is already mature, so that this plant is protogynous. Both protandrous and protogynous dichogamy may be complete or incomplete. It is *complete* when the stigma begins to ripen after the removal of the pollen from the adjoining anthers by wind or by flower-visiting insects, so that it can no longer fertilize its own flower; or if the stigma is withered, dried up, or fallen away as soon as the anthers of the same flower open and expose the pollen or scatter it abroad, as in the Wall Pellitory (see figs. 291 [2, 3, 4]). Dichogamy is *incomplete* when the ripening of the two kinds of sexual organs is not, indeed, simultaneous, but when the capacity for fertilization of one sex is not at an end before the other sex in the same flower is mature. There are, of course, many grades in incomplete dichogamy. In long-lived flowers the start which one sex has over the other may amount to several days, but in short-lived flowers it may be limited to a few hours. Cruciferæ all have protogynous flowers. The already mature stigma is visible in the centre of the flower as soon as the petals open, but the surrounding anthers are still shut up. This only lasts for a short time; soon the anthers dehisce, and then both sexes come into operation. In *Lepidium Draba*, *Sisymbrium Sophia*, and numerous other species, this difference of time (lasting from the moment when the stigma is accessible to the moment when the anthers begin to shed the pollen) is only 2–5 hours. The same may be said of numerous Rock-roses, Papaveraceous plants, Cactuses, Ranunculaceæ, Rosaceæ, Boraginaceæ, Gentianaceæ, Ericaceæ, and Valerianaceæ (e.g. *Helianthemum alpestre*, *Glaucium luteum*, *Opuntia nana*, *Actæa spicata*, *Adonis vernalis*, *Atragene alpina*, *Clematis Vitalba*, *Potentilla caulescens*, *Cynoglossum pictum*, *Lithospermum arvense*, *Menyanthes trifoliata*, *Arctostaphylos uva-ursi*, *Vaccinium Myrtillus*, *Valerianella dentata*). Even the majority of ephemeral flowers exhibit dichogamy. The flowers of the Marvel of Peru (*Mirabilis Jalapa*) open between seven and eight o'clock in the evening; as soon as the margins of the flower unfold, the small stigma, resembling a tiny brush, is able to receive pollen, but the anthers are as yet entirely closed. About 10–15 minutes later the anthers dehisce and shed their pollen. The difference in the time is so slight here that it would be unnoticed by most people, and this explains why such flowers have not been regarded as dichogamous. But the very circumstance that the maturation of the two kinds of sexual organs is not simultaneous, even in ephemeral flowers, is of the greatest importance for the question of the significance of dichogamy and must be especially dwelt upon here.

In protogynous dichogamy it is no uncommon thing for the stigma to project from the flower already fitted to receive pollen whilst the petals are still closely shut, the whole flower having the appearance of a bud. This happens in the Curled Pondweed (*Potamogeton crispus*, figured on p. 148), in Asphodels (e.g. *Asphodelus albus*), in Woodrushes (e.g. *Luzula nivea*), in Elms (e.g. *Ulmus campestris*), in the Plantain (e.g. *Plantago media*), in several Rhododendrons (e.g. *Rhododendron Chamæcistus*), in *Cortusa, Deutzia*, and many other plants. On the other hand, many plants with protandrous dichogamous flowers are known where the pollen is shed from the anthers while the petals are still folded as in the bud. On opening the ripe bud of *Crucianella stylosa* (figured on p. 265), it can be seen at a glance that the anthers have already dehisced some little time, and have deposited their pollen under the dome of the closed bud on the thickened warty surface at the end of the style. In the flowers of *Rhododendron hirsutum*, the pollen falls from the anthers while still in the bud, and the same may be observed also in many Composites, Campanulaceæ, and Papilionaceous flowers.

We are not yet in a position to say whether protandrous or protogynous species are the more abundant, although the dichogamy of thousands of plants has been investigated. By generalizing on this subject one is liable to fall into very great error. It would be particularly dangerous to generalize prematurely on the results which have been obtained from the examination of many species of a genus, or many genera of a family, and to consider them to hold good for the whole group, for most genera contain some protandrous species, even when the majority of them are protogynous, and *vice versâ*. Liliaceous plants are described as protandrous in most Botanical books, but in reality many of the genera and species are incompletely protogynous (*Amaryllis, Asphodelus, Colchicum, Erythronium, Leucojum, Lilium Martagon, Narcissus poeticus, Ornithogalum umbellatum, Scilla, Trillium,* &c.). Among the Umbelliferæ, which are usually stated to be all protandrous, there are quite a number of protogynous genera and species, as, for example, *Æthusa, Astrantia, Caucalis, Eryngium, Hacquetia, Pachypleurum, Sanicula, Scandix*, and *Turgenia*. This also applies to the Saxifrages: the majority, of course, are protandrous, but some of them, viz. *Saxifraga androsacea* and *peltata* are decidedly protogynous. The large-flowered species of Crane's Bill (*Geranium argenteum, lividum, pratense, sylvaticum*) are protandrous, the small-flowered (*Geranium columbinum, lucidum, pusillum, Robertianum*) are protogynous. In the Scrophulariaceæ the genera *Digitalis* and *Penstemon* are protandrous, and the genera *Linaria, Pæderota, Phygelius, Scrophularia, Veronica* protogynous. Of species belonging to Boraginaceæ some are protandrous (e.g. *Borago, Echium*), others protogynous (e.g. *Cynoglossum, Lithospermum*). In Ranunculaceæ the genus *Aconitum* is protandrous, while the genera *Adonis, Anemone, Atragene, Clematis*, and *Pæonia* are protogynous. In the Gentian family some are protandrous, viz. *Swertia perennis, Gentiana asclepiadea, ciliata, cruciata, Frœlichii, Pannonica, Pneumonanthe, punctata*, and *prostrata*; others, especially *Menyanthes trifoliata, Gentiana Bavarica, Germanica, glacialis, Rhætica*, and *verna* are protogynous. The same is true of Ericaceæ, Valerianaceæ, Polemoniaceæ, and many other groups. As far as we know, the Composites, Campanulaceæ, Labiatæ, Malvaceæ, Caryophyllaceæ, and Papilionaceous plants are exclusively protandrous, Rushes and Woodrushes (*Juncus* and *Luzula*), Aristolochiaceæ and Thymelaceæ, Caprifoliaceæ, Globularias, Solanaceæ, Rosaceæ, Berberidaceæ, and Cruciferæ exclusively protogynous.

It has already been pointed out that the non-simultaneous maturation of the sexual organs goes hand in hand with the separation in space of the two sexes in most instances, or, in other words, that in plants where the two kinds of sexual organs have in any way been separated from one another in the flowers by actual distance, dichogamy also obtains. Thus, for example, it appears that all species of plants whose hermaphrodite flowers are adapted to cross-fertilization by the relative position and arrangement of their two kinds of sexual organs, or by the interchange of position of anthers and stigmas are, moreover, dichogamous, although this dichogamy may be only of slight duration. Plants with heterostyled flowers are also dichogamous, since those with short-styled and those with long-styled flowers develop at different times. If one observes the many hundred individuals of *Primula Auricula*, growing side by side on a rocky crag under the same conditions, it is easy to see that the plants with long-styled flowers are earlier than those with short styles. The former are already over while the latter are in full bloom. The reverse is the case in *Auricula longiflora*; here plants with short-styled flowers are in full blossom when the long-styled flowers of the neighbouring plants are still in bud.

Plants bearing pseudo-hermaphrodite flowers are also dichogamous. The Valerians (*Valeriana dioica, polygama,* and *tripteris*) open their pistillate flowers 3–5 days before their staminate flowers in the same locality; these plants are therefore decidedly protogynous. In the Alpine Dock (*Rumex alpinus*), the stigmas of the pistillate flowers are ripe 2–3 days before the anthers of the staminate flowers and of the truly hermaphrodite flowers on the same plant have opened. In the Ash (*Fraxinus excelsior*), the stigmas of the pistillate flowers are mature whilst the anthers in the neighbouring staminate and hermaphrodite flowers are still closed. The latter do not usually shed their pollen till 4 days later. The dichogamy of the Grasses, which bear both true staminate and hermaphrodite flowers, is very striking (e.g. *Anthoxanthum odoratum, Hierochloa australis, Melica altissima,* and *Sesleria cœrulea*). In these plants the anthers do not liberate their pollen until the neighbouring stigmas have been mature for two days. This may also be observed in Composites whose capitula contain true hermaphrodite and pistillate flowers, and in those with true pistillate and pseudo-hermaphrodite male flowers. The stigmas of the pistillate flowers are already mature two days before any pollen can be obtained from the adjoining truly hermaphrodite or staminate flowers. It will suffice to mention as examples of this *Aster alpinus, Aronicum glaciale, Bellidiastrum Michelii, Doronicum cordatum, Erigeron alpinum, Gnaphalium Leontopodium, Tussilago Farfara,* and *Calendula offici-*

nalis. Labiates which bear only true hermaphrodite flowers on one plant, and only pseudo-hermaphrodite female flowers on another are protogynous. In the Marjoram (*Origanum vulgare*), the pistillate (pseudo-hermaphrodite female) flowers are ripe as much as eight days or longer before the true hermaphrodite flowers. The fact must be emphasized that these remarks only refer to such flowers or plants as develop under similar conditions of life, and that they are not applicable to instances where the early or late maturity depends upon whether the habitat is a sunny or shaded one.

As far as we can tell at present all monœcious plants are protogynous. Sedges, Bulrushes, Bur-Reeds (*Carex, Typha, Sparganium*), Aroids with monœcious flowers, the Maize (*Zea Mays*), the monœcious Stinging Nettle (*Urtica urens*), the Water Milfoil (*Myriophyllum*), the Burnet (*Poterium*), the Burweed (*Xanthium*), the monœcious Euphorbiaceæ (*Euphorbia, Ricinus, Buxus*), and especially Alders and Birches, Walnuts and Planes, Elms and Oaks, Hazels and Beeches, are all markedly protogynous. In most of these plants, especially the last-named trees and shrubs, the dust-like pollen is not shed from the anthers until the stigmas on the same plant have been matured 2–3 days. Sometimes the interval between the ripening of the sexes is still greater. The majority of diœcious plants also are protogynous. In the luxuriant Willows on the banks of rivers a single species is sometimes represented by thousands of bushes. Some of them bear staminate, the others pistillate flowers. They grow on the same soil, are exposed to the same amount of sunlight, and are fanned by the same breezes, and yet, in spite of identical external conditions, the plants with pistillate flowers certainly precede their staminate neighbours. The stigmas of the Almond Willow (*Salix amygdalina*) are already mature 2–3 days before a single anther of this species has dehisced anywhere. The same happens in the Purple-willow, Osier, and Crack-willow. This phenomenon can also be observed in the sub-alpine Willows (*Salix herbacea, retusa, reticulata*), but here the difference in time is usually restricted to a single day. Among the countless plants of Hemp (*Cannabis sativa*), which grow up together in the summer in closest proximity from seeds sown on level fields, most of the individuals which bear pistillate flowers have already protruded their stigmas before a single staminate flower has opened. The latter do not unfold until 4–5 days after the pistillate plants have begun to blossom, and then only does the wind scatter the pollen from their versatile anthers. In the Dog's Mercury, especially in the perennial species of the genus (*Mercurialis ovata* and *perennis*) which grow in small clumps in the depths of our woods, plants with pistillate and others with staminate flowers being close together on the same soil, the stigmas are capable of fertilization at least two days before the pollen is shed. The same thing is observed in the Hop (*Humulus Lupulus*), and in many other diœcious plants.

All these facts are of the greatest importance in the question of the significance of cross-fertilization. If the maturation of the sexes at different times had been observed only in those species of plants which bear hermaphrodite flowers, dichogamy might be regarded merely as the completion of the contrivances for preventing the pollen from fertilizing the stigmas of the same flower, *i.e.* for preventing self-fertilization or autogamy. For example, the relative position of the anthers and stigmas in the flowers of the Arrow-grass (*Triglochin*; see fig. 237, p. 149) renders it almost impossible for the pollen to reach the stigmas in the same flower, but the possibility would not be excluded were the anthers to shed their pollen at the time when the stigmas were capable of being fertilized. Since, however, in the flowers of the Arrow-grass, the stigmas are quite dried up at the the time of dehiscence, autogamy is quite impossible, and so far dichogamy is a completion of the contrivances mentioned. But such cases of complete dichogamy as in the Arrow-grass, the Wall Pellitory, and the Grass of Parnassus, &c., are comparatively rare, and this explanation will not hold for the great bulk of hermaphrodite flowers which are incompletely dichogamous. Still less will it apply to monœcious and diœcious plants. Here there is no question of autogamy or self-fertilization, and for this reason all hypotheses founded on the prevention of self-fertilization by dichogamy are futile.

We cannot suppose, however, since the non-simultaneous maturation of the sexes is a phenomenon which occurs in most—perhaps in all—plants, that this contrivance has no meaning. I will now endeavour to elucidate the significance of dichogamy and invite the reader, first of all, to enter one of the Willow plantations which have been briefly described above. The Purple Willow (*Salix purpurea*) is just beginning to bloom. The pistillate flowers already display mature stigmas; but the staminate flowers are still behind, and not a single anther has opened. The staminate flowers of the Osier (*Salix viminalis*), on the other hand, growing in the same clump with the Purple Willow, are in their prime. The pollen of the Osier is to be had in any abundance. Numerous bees have been attracted by the scent and colour of the male catkins, and they buzz from bush to bush, sucking the honey and collecting pollen. They are not dainty in their work, and do not limit themselves to one species but fly impartially to the Purple Willow, to the Osier, or to other species of Willow which may happen to be present. Now, if a bee comes to suck the honey from the pistillate flowers of the Purple Willow, after it has just visited another Willow bush, where it has covered itself with pollen, obviously that bush must have been the Osier, Sweet Willow, Sallow Willow, or some other species, whose staminate flowers have already developed so far as to render their pollen accessible. It cannot have been a Purple Willow, because not a single anther of this species in the whole neighbourhood has yet opened. But since the stigmas of the Purple Willow are thus fertilized by the pollen of the Osier, &c., hybridization occurs. Two or three days later, a legitimate crossing may take place, for, by this time the anthers of the Purple Willow will have protruded from the staminate flowers and opened widely, and abundance of pollen will be afforded to insects. These are not slow to visit the now accessible flowers, and they remove some of the pollen and transfer it to the stigmas of the same species which are still capable of being fertilized. Thus at the commencement of flowering hybridization is alone possible, and legitimate cross-fertilization cannot take place till some time later, in consequence of the dichogamy of these Willows. This obviously applies to all other Willows, and generally to all diœcious plants whose flowers are incompletely protogynous.

In order to show that the same processes obtain in monœcious plants, I would ask the reader to accompany me to the edge of a moor where numerous monœcious Sedges (*Carex*) form the chief constituents of the vegetation. Widely different species grow in varied profusion side by side. Here at the margin of a dark pool *Carex acutiformis, filiformis, riparia, vesicaria, paniculata,* there, on the marshy stretch close by, *Carex flava, canescens, glauca, Hornschuchiana,* and many others. These Sedges do not all blossom at the same time; one ceases to flower just when another is in its prime, and when, in a third sort, the flowers have just begun to fade. All monœcious Sedges are protogynous. The stigmas have been ripe 2–3 days, and have protruded far beyond their subtending bracts, so that it would seem natural that the pollen, wafted by the wind, would remain attached to them. But the anthers of the staminate flowers of the same species have not yet opened. It is evident then that the stigmas must be pollinated during the first and second day with pollen from other species which blossom earlier, for since the anthers of these earlier species are already open, each gust of wind will shake out their pollen and blow it over the moor, pollinating everything which is capable of being pollinated. The pollen of the same plants (afterwards shed from the staminate flowers above and close to the mature stigmas) can only be received in the second place on account of its later arrival. Thus, we see that incomplete dichogamy promotes hybridization in the first place, and then, only later, a legitimate cross-fertilization in plants with monœcious flowers.

It is well known that all the plants of a species growing under similar external conditions do not blossom on the same day, and this fact is worth noticing in so far as it might be thought possible for the earlier plants of a species to provide pollen for the stigmas of later plants. This is certainly often the case, but it is also certain that the stigmas of the very earliest plant of a protogynous species can only be, and actually are, fertilized with pollen from another species which flowers still earlier; thus the conclusion already arrived at must remain unaltered.

It may be taken for granted, since plants with pseudo-hermaphrodite flowers behave exactly like diœcious and monœcious flowers in the manner of the transfer of their pollen, that their dichogamy has the same significance. The spikes of Docks belonging to the group *Lapathum*, viz. *Rumex alpinus, nemorosus,* and *obtusifolius,* bear principally pseudo-hermaphrodite flowers, which are some of them male, some female, and besides these a few true hermaphrodite flowers. In any one plant, the development of the stigmas is always considerably in advance of that of the anthers. The stigmas are ripe whilst the anthers are still closed. Under these circumstances the first flowers of a plant, whether pseudo- or truly hermaphrodite, can only receive pollen from other plants which have been in bloom for several days, and whose dehisced versatile anthers have been robbed of their pollen by the wind. It may further be taken for granted that any hundred plants of *Rumex obtusifolius,* growing together in a clump, will not all blossom together, and consequently innumerable crossings take place between the flowers of the individuals of this same species. The first ripe stigmas of the earliest plants of *Rumex obtusifolius* within an hour's walk can only receive their pollen during the first two days from other species of Dock, and therefore, when they first blossom, hybridization only can occur. It has already been stated that plants of Marjoram (*Origanum vulgare*, a Labiate), which bear pseudo-hermaphrodite female flowers, blossom fully eight days before those with truly hermaphrodite flowers. To this we might add that the plants which blossom first in any given district cannot obtain pollen from the same species, and that consequently, if the stigmas are, nevertheless, pollinated by insects, the pollen must have been obtained from some other species. In Compositæ, whose capitula contain both truly hermaphrodite and pseudo-hermaphrodite female flowers, the latter always mature some days before the former, and consequently the pioneer flowers in a given locality can only obtain pollen from species which bloom still earlier, so that again hybridization occurs. In the floral region of the Black Sea many Fleabanes grow side by side (*Inula Oculus-Christi, ensifolia, Germanica, salicina*, &c.), and in the summer they blossom in definite succession, so that one species always begins to fade when another is in its prime. Each capitulum of these Inulas consists of tongue-shaped pseudo-hermaphrodite female flowers on the circumference and tubular hermaphrodite flowers in the centre. The former unfold earlier than the latter, and for each species there is a certain period, if only two days, when the pollen, brought by insects to the stigmas of the pistillate flowers on the circumference, can only have been obtained from another species, since their own pollen is not obtainable. Many other examples of the same kind might be quoted, all pointing to the fact that hybridization at the commencement of flowering and the subsequent legitimate crossing depend mainly on the incomplete dichogamy obtaining in these plants.

It is the same with plants which have true hermaphrodite flowers. In heterostyled species either the long-styled or the short-styled flowers may develop first. The long-styled flowers of *Primula Auricula* and the short-styled flowers of *Primula longiflora* are the earlier, consequently, the stigmas of the first long-styled *Primula* plants can only be fertilized with pollen from other species. This is often actually effected by insect-agency, and gives rise to numerous *Primula* hybrids. The same thing is repeated in hermaphrodite flowers which are not heterostyled. When a plant is protogynous, as, for example, the open-flowered Pasque-flower, *Pulsatilla patens*, the earliest flowers can receive no pollen from anthers of their own species, because not one is open, but it would be possible for them to be provided with the pollen of other species of the same genus which inhabit the same locality but blossom earlier. This, of course, only holds good for the *commencement* of the flowering period, and only for those plants of the species which are the first to open their flowers in a given place. At a later period of flowering legitimate crossing will occur, because by that time the earliest plants have shed their pollen, and it may be collected and transferred by insects. Among hermaphrodite plants there are many whose flowers are not protogynous but protandrous. Here the stigmas of the earliest flowers of a species cannot be pollinated, because they are immature and inaccessible. What, then, becomes of the pollen of these first protandrous flowers? If it is carried by the wind or by insects, as soon as it is liberated from the anthers, to any stigma, that stigma must of necessity belong to another species which has already become receptive. Towards the end of the flowering period, the pollen usually runs short in most protandrous species, whilst the stigmas of these stragglers have only just attained maturity. They could only obtain pollen from flowers which had not developed so far. But if these flowers are the last in the locality, and they are protandrous, there is no more pollen to be had from that species, and obviously they must be satisfied with pollen from some other. Accordingly hybridization is a matter of necessity in the latest flowers of hermaphrodite plants which are protandrous, just as it is in the earliest flowers of those which are protogynous.

From these facts we may infer that every dichogamous plant has an opportunity for illegitimate crossing or hybridization at the beginning or end of its flowering, and that dichogamy—especially incomplete dichogamy—is the most important factor in its production. Of course this does not exclude dichogamy from playing an important part in legitimate crossing as well. On the whole, however, we can maintain the view that the separation of the sexes by the maturation of the sexual organs at different times leads to hybridization, whilst their separation in space promotes legitimate crossing. The fact that the separation of the sexes in time and space usually occur in conjunction, harmonizes with this conclusion, *i.e.* that the diœcious, monœcious, and pseudo-hermaphrodite flowers, as well as those hermaphrodite flowers whose sexual organs are separated by some little distance, are in addition incompletely dichogamous, because by this contrivance the flowers of any species obtain (1) the possibility of hybridization at the beginning or end of their flowering period, and (2) of legitimate crossing during the rest of that time. This also explains why incomplete dichogamy is so much more frequent than complete dichogamy; why there are no diœcious species of plants with completely dichogamous flowers; and why, if one ever should occur, it would of necessity soon disappear. Let us suppose that somewhere or other there grows a species of Willow with completely protogynous diœcious flowers, that is to say, a species in which the female flowers mature first, and have ceased to be receptive before the male flowers in the same region discharge their pollen. Hybridization only could occur in it, and the young Willow plants resulting from it would all be hybrids whose form would no longer agree absolutely with that of the pistilliferous plant. The species would therefore not be able to reproduce its own kind by its seed, and it would leave no descendants of similar form; in other words, it would die out.

Two varieties of legitimate crossing, caused by the separation of the sexes by actual distance, have already been mentioned (see p. 301), viz., *Xenogamy* and *Geitonogamy*. We speak of xenogamy (from ξένος, a stranger, and γάμος, marriage) when the flowers in question belong to different individuals of the same species, and of geitonogamy (from γείτων, a neighbour, and γάμος, marriage) when the two flowers are on the same plant. We cannot, however, draw a sharp line between the two. The offshoots of a plant, which become ultimately isolated, forming independent plants, are, in point of origin, identical with the branches of a plant which remain attached. Accordingly, when a crossing occurs between flowers produced on plants that have arisen from one another by offshoots, the process is not essentially different from the crossing which takes place between flowers on adjacent branches. It is nevertheless convenient to keep the two cases distinct, on account of certain processes connected with the greater or lesser distances between the flowers.

Both in xenogamy and geitonogamy the transport of the pollen is effected partly by wind and partly by flower-visiting insects. How this is carried out, and the endless variety which exists, has been dealt with in detail in previous chapters. Geitonogamy is not infrequently, however, brought about in other ways, as by the pressing of mature stigmas on the liberated pollen of neighbouring flowers, or by the actual falling of pollen upon them. Since these methods of cross-pollination have only been incidentally touched upon, they must be described here somewhat more fully.

The conditions for crossing between neighbouring flowers are simple when the flowers are crowded in heads, umbels, bunches, spikes, and the like, standing so close together that the stigmas of one flower can easily touch the pollen-covered anthers of another. And since this kind of crossing is actually very widespread and is repeated in certain species with great regularity, generation after generation, we are justified in regarding these forms of inflorescence as being particularly associated with geitonogamy, and in assuming that a not unimportant advantage of a crowded inflorescence lies in the possibility of crossing between the neighbouring flowers of a plant (see vol. i. p 740).

As we might expect, this particular form of crossing occurs with great frequency in Compositæ, whose flowers are crowded so densely into capitula that the whole inflorescence might be taken, at first sight, for a single flower; consequently this extensive family of plants, which includes more than 10,000 species, will be the most suitable in which to describe the phenomenon of geitonogamy. We will commence with those Composites whose heads only contain "ray" or ligulate florets. The term ray or ligulate floret is applied to florets whose corolla is tubular only at the base, the free end being flattened and projecting outwards like a tongue or strap, as in the Dandelion. In *Prenanthes* each capitulum consists of only five such ray-florets. In each floret the long, thin style is inclosed in a tube of anthers. The style is covered with stiff outwardly-directed bristles which are called "sweeping hairs". When the style elongates, immediately after the opening of the flower, these hairs sweep out the pollen which has been already shed into the interior of the anther-tube. The long style, rendered quite yellow by the pollen it carries, now projects from the empty tube of anthers. The two branches of the style which bear the stigmatic surface are at first folded together, but they soon separate, and the stigmas can then be fertilized by the aid of insects with pollen brought from other plants, but not with that which lies on the sweeping hairs below the stigmas. As soon as the strap-shaped corollas begin to wither and shrivel, the two stylar branches diverge strongly, and twist and turn like tiny snakes sideways and downwards. At the same time adjacent styles come nearer to one another, and it is therefore natural that the stylar branches of neighbouring flowers should get entangled. In this way the stigmas of one flower (which are still in a receptive state) necessarily come in contact with the pollen on the sweeping hairs of another, and pollination ensues.

The same process occurs in the flowers of the Lettuce (*Lactuca*), the Alpine Sow-thistle (*Mulgedium*), and in *Chondrilla*, only here the heads contain more florets than in the form just described. The stylar branches do not undergo snake-like movements, but they diverge widely and roll back a little, an action altogether sufficient to bring them into contact with the styles of neighbouring flowers and to promote a crossing. It is worth noticing that the corollas of the ray-florets of *Prenanthes* roll outwards when they begin to fade, while those of the Lettuce and of the other Composites mentioned fold up and form a hood over the stylar branches during crossing. The Salsify (*Tragopogon*), Hawkweed (*Hieracium*), *Crepis*, *Scorzonera*, Hawkbit (*Leontodon*), Dandelion (*Taraxacum*), and many other Composites, of which these plants may be regarded as typical, contain in each head as many as 100 ray-florets arranged in spiral series (*cf.* fig. 222[5], p. 112). The strap-shaped corollas separate in the morning and fold together in the evening, and similarly the anther-tubes and styles are inclined somewhat to the circumference of the capitulum in the morning, but come close together and assume an upright position in the evening. This gradual approach ultimately becomes actual contact, and since the development of the protandrous florets proceeds from the circumference towards the centre of the capitulum, the stigmas of the outer florets are mature at the time when the pollen has only just been swept out of the anther-tubes of the inner florets. The contact of the adjoining flowers, therefore, necessarily leads to cross-pollination. The fact that the corollas of the ray-florets in any capitulum are of unequal length (fig. 222[5], p. 112) has also a close bearing on this process. If they were all equally long this contact and crossing would be impossible, for division walls would be interposed between the styles of the outer and inner florets. But the inner corollas are just short enough to allow the styles to touch one another. In many of these plants, *e.g.* in the Salsify (*Tragopogon*), geitonogamy is also assisted by the arrangement of the flowers in each capitulum, each flower of an outer row being placed exactly between two of the next inner series. When the capitulum closes, the two curved stylar branches of an outer floret, with their exposed stigmatic surfaces, become applied to the pollen-covered styles of the inner flowers immediately to right and left in front of them.

There are comparatively few species of Composites having exclusively tubular florets in which cross-pollination occurs between the members of the same capitulum. The most remarkable of these species belong to the Hemp Agrimony genus (e.g. *Eupatorium aromaticum* and *cannabinum*; see figs. 294[1] and 294[2]). The capitula contain but few florets; those of *Eupatorium cannabinum* have five, which open one after another in the course of 5–8 days. Younger and older flowers are therefore always close together. The styles are rather different from those of other Composites, being divided almost half-way down into two long threadlike branches which bear the stigmatic tissue only on their lower portions. The rest of the branch is thickly studded with short bristles, the aforesaid sweeping hairs. The styles are parallel and folded together as long as they are inclosed in the anther-tube (see fig. 294 ²), and they remain closed for some time after they have elongated and pushed their way above the anthers. During the elongation the sweeping hairs brush the pollen from the anther-tube, and it then adheres in abundance to the outer side of each style-branch. This condition, however, does not continue for long. The stylar branches soon diverge at an angle of 40–50°. The branches of adjacent styles now cross one another like rapiers, and when the pollen is detached from the sweeping hairs it falls on to the mature stigmatic tissue. The closed pollen-covered stylar branches, as they emerge from the anther-tube, come in contact with the divergent branches of older neighbouring florets, and thus the pollen is transferred to the stigmatic tissue of the latter.

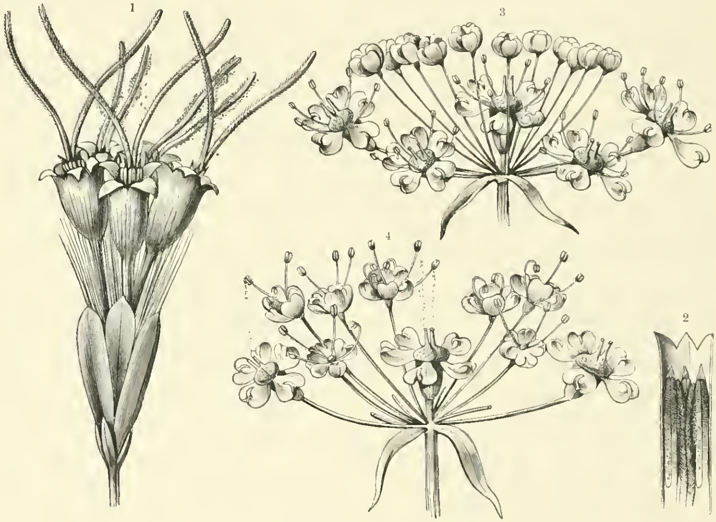


Fig. 294.—Geitonogamy with adherent pollen.

¹ Crossing of the stylar branches of neighbouring florets in the capitulum of *Eupatorium cannabinum*. ² Longitudinal section through the upper part of a floret of *Eupatorium*; the two stylar branches are parallel and inclosed by the anther-tube, which is again surrounded by the corolla-tube. ³ Umbel of *Chærophyllum aromaticum*; the truly hermaphrodite flowers are open, the pseudo-hermaphrodite male flowers are still closed. ⁴ The same umbel; the true hermaphrodite flowers have lost their pollen; the male flowers are now open, and their anthers drop pollen on the stigmas of the hermaphrodite flowers. All the figures somewhat enlarged.

The capitula of the Colt's-foot (*Tussilago*) and of the Marigold (*Calendula*) contain two kinds of florets. In the centre are pseudo-hermaphrodite male flowers, whilst true pistillate ray-florets form the fringe of the capitulum. The latter open earlier than the disc-florets, and therefore at first can only be fertilized with pollen from other capitula which are further advanced. But soon the pollen is pushed out of the disc-florets of the same capitulum, and is deposited in a small clump at the top of the anther-tube. This pollen is conducted to the stigmas of the neighbouring ray-florets by different methods in the two genera mentioned. In the Colt's-foot the numerous ray-florets at the periphery are expanded horizontally during the daytime, but towards evening they fold up, and in this way, as they bend over the tubular florets, contact with their clumps of pollen is unavoidable. The pollen is transferred to the ray-florets, and when the capitula open again next morning, and the ray-florets bend outwards, the adherent pollen is freed, and slips down to the ripe stigmas at the base of the corolla. The process is far simpler in the Marigold. The stylar branches of the ray-florets are bent inwards over the adjoining disc-florets while the latter are still closed. When they open, and the pollen is swept out of their anther-tubes, it of course passes inevitably to the stigmas of the neighbouring ray-florets which are situated just above.

The Golden-rod (*Solidago*), Aster (*Aster*), and many other Composites classed together in the group of the Asteroideæ, closely resemble the Colt's-foot and Marigold in outward appearance, but their sexes are differently arranged. The tubular disc-florets are all truly hermaphrodite, and the outer ray-florets are truly pistillate. The latter mature first, and are adapted to hybridization, as we have already remarked. Two days later the hermaphrodite flowers of the disc open—those towards the circumference being the first. Their pollen is pushed out, and meanwhile the flowers bend slightly outwards, so that the pollen lying on the anther-tubes in the form of small clumps either comes into direct contact with the ripe stigmas of the marginal ray-florets or falls on to them from a short distance.

In very many Composites the capitulum contains only hermaphrodite flowers with tubular corollas. The development of the flowers again proceeds from the circumference towards the centre of the capitulum, and in each flower, soon after the corolla has opened, the pollen is swept and pushed out of the anther-tube by the sweeping hairs or warts on the outer side of the style. The pollen forms a small clump at the mouth of the anther-tube, but does not retain this position long. The two stylar branches which have hitherto been folded together (their outer surface being coated with pollen) soon separate and often bend back in a curve so as to expose their ripe stigmatic surfaces. The pollen is thus for the most part detached in small crumbling balls which simply tumble down. In this way they reach the ripe stigmatic tissue of the older neighbouring flowers and geitonogamy ensues. Various contrivances are met with in these Composites to prevent the pollen which falls from the younger flowers from missing its mark, and to ensure its arrival on the stigmas of the nearest older flowers. In *Homogyne alpina* (an alpine plant related to the Butterbur) the tubular florets on the flat receptacle of the capitulum are of unequal length. The marginal florets are rather shorter than the central ones, so that the stylar branches of the former are lower than those of the latter. But this is not enough to bring the pollen which has fallen from the higher stylar branches on to the stigmatic tissue of these older lower ones—since the lower are situated rather nearer the circumference of the capitulum, and it is therefore necessary that the pollen-bearing styles should incline outwards if their pollen is to reach its proper destination. This is what actually happens. The originally straight and erect styles bend outwards at an angle of 70–90°, even before their branches have separated, and while they yet retain the pollen which they have collected from the anther-tubes. When it is thrown off, it thus unavoidably reaches the lower stigmas of the older flowers. Or sometimes it happens that the divergent stylar branches of the younger flowers with attached pollen come into direct contact with the stylar branches of older flowers, and that geitonogamy is effected in this way.

Numerous other Composites whose capitula are composed entirely of tubular hermaphrodite flowers exhibit the same processes as *Homogyne*, which has been chosen here as a type. The Wormwoods of mountain heights, e.g. *Artemisia Mutellina* and *spicata*, exhibit a slight deviation. In them the central florets are raised above the marginal ones, not only by their greater length, but because the receptacle on which they stand is considerably arched. Obviously the florets at the top of the dome will stand higher than those round its circumference. In very many Composites (*e.g.* in *Doronicum glaciale* and *scorpioides*, in *Senecio cordatus*, in *Telekia*, *Buphthalmum*, *Anthemis*, and *Matricaria*), the receptacle is at first flat or but slightly arched; but during the flowering period it rises up so much that it assumes the form of a hemisphere, or even of a cone. This elevation in *Doronicum*-capitula, for example, amounts to 1 cm., and it is relatively even more in species of *Anthemis* and *Matricaria*. The immediate consequence of this change in the receptacle is of course an alteration in the direction of the flowers which stand on it. Flowers which stood erect on the receptacle of the capitulum when it first opened, assume later an almost horizontal position. But the most remarkable thing is that these changes keep pace with the advancing development of the flowers. In capitulate inflorescences the marginal flowers open first, and those in the centre last (see vol. i. p. 740). The flowers of each outer series are therefore always further advanced than those of the adjoining inner series, and when the mature stigmas are already opened in the outer flowers, the pollen of the inner ones is only just being pushed out of the anther-tubes and shaken off the stylar branches as they separate. A wonderful contrivance now meets our gaze—the mature stigmas of the outer flowers are brought directly under the inner flowers so as to catch their pollen as it falls, a condition brought about by the alteration in form of the receptacle on which all the flowers stand. Sometimes the pollen does not need to fall, for the flowers stand so closely side by side and above one another that the divergent stigmas of the older flowers come at once into direct contact with the pollen of the younger flowers. This is the case in various species of the Groundsel genus (*Senecio*) where the two stylar branches diverge, not in a horizontal but in a vertical plane, the consequence being that one of the stylar branches comes in contact with the clumps of pollen just pushed out from a neighbouring higher flower. Of course there exist among Composite flowers quite a number of forms intermediate between those here described, all of which promote geitonogamy, but we cannot enter upon them further.

Among Umbelliferous plants, as in Compositæ, the numerous small flowers are crowded so closely together that the stigmas and pollen of neighbouring flowers can easily touch and combine, and a glance at these inflorescences is enough to suggest the possibility of geitonogamy. The conjecture is confirmed on a closer scrutiny, for the Umbelliferæ, as a matter of fact, exhibit an even greater variety of contrivances for geitonogamy than do the Compositæ. The most important of these will now be detailed. First, let us examine the group which is typified by the genera *Eryngium* and *Hacquetia.* In these the flowers are crowded together in capitulate masses surrounded by broad conspicuous bracts. They are all hermaphrodite and protogynous. The stamens with closed anthers are bent inwards in each flower like hooks, and the petals are still unfolded, but the sticky, shining stigma on the top of its long style already projects some distance out of the bud. At this stage the stigma can only be pollinated with pollen from other plants, indeed, from other species. Later, the stamen-filaments elongate and straighten, whilst the anthers dehisce, and pollen appears through the clefts. This pollen comes into contact either at once or very soon with the still receptive stigmas; for the long styles have meanwhile inclined more to the 'side, so that their stigmas are placed in such a position with regard to neighbouring flowers that either they brush against the pollen-covered anthers, or else are pollinated with the crumbling pollen which falls from these anthers.

The genera *Sanicula*, *Astrantia*, and *Laserpitium*, differ somewhat from this group of Umbelliferæ. The chief modification is that in the species of these three genera staminate as well as hermaphrodite flowers occur. In *Sanicula* each umbel consists of 3 true hermaphrodite flowers in the centre, and 8–10 staminate flowers arranged round them like a wreath. The hermaphrodite flowers are protogynous and the first to develop, so that at the beginning of flowering the stigmas can only be fertilized with the pollen from plants of other species. The stamens straighten afterwards and project like the style far out of the flowers. But the anthers and stigmas of the same flowers do not touch, since the styles stand up erect, whilst the stamens have an oblique direction. A crossing soon takes place, however, between the hermaphrodite flowers and the adjoining staminate flowers, in the following way. The stamens of the hermaphrodite flowers wither and fall off, and the stigmas of these flowers become divergent, curving slightly outwards, so that their still receptive surfaces are brought into the surrounding circle of stamens. The anthers of the male flowers have meanwhile dehisced and are shedding abundant pollen. The stigmas are necessarily pollinated either by the direct contact of stigmas and anthers, or, by the falling of the pollen from these anthers. The arrangement of the flowers in *Astrantia* has already been described on p. 296; it agrees with *Sanicula* in having hermaphrodite and staminate flowers in each umbel, the hermaphrodite flowers developing first and being protogynous, so that again the sticky stigmas of the first-opened flowers in a given locality can only be fertilized by the pollen of other species. Later, the stigmas of the hermaphrodite flowers separate, and to a certain extent offer themselves to the pollen of the neighbouring staminate flowers which is now being shed. *Laserpitium* exhibits the same general arrangement of flowers as *Sanicula* and *Astrantia*, but the hermaphrodite flowers in the large, loose umbel are protandrous instead of protogynous. Geitonogamy, however, obtains, just as in *Astrantia*, by the stigmas at the top of the divided style exposing themselves to the pollen from the anthers of the neighbouring staminate flowers. Since the protandrous hermaphrodite flowers open before the staminate ones, their stigmas are mature exactly at the same time that the anthers of the latter shed their pollen.

A notable exception to these Umbelliferæ which have been described, where the stigmas of one flower obtain the pollen from neighbouring flowers by the elongation and bending of their styles into their neighbour's domain, thus producing geitonogamy, is afforded by others whose styles and stigmas retain their original position. The stamens, however, elongate and straighten, and assume such a position that the pollen liberated from their anthers can reach the stigmas of the neighbouring flowers. One group of such species, of which *Pachypleurum*, so abundant on the mountain heights of Europe, may serve as a type, develops a single flat umbel at the end of the stalk bearing flowers all hermaphrodite. They are also protogynous —their sticky stigmas can receive pollen, while their anthers are still closed. When flowering first begins, therefore, crossing can only be with other plants. Then the stamens straighten and stand out on all sides like a star till the long filaments place their anthers in the line of the neighbouring flowers. Since the stigmas are still receptive some of the pollen falling out of the bursting anthers inevitably reaches the stigmas of one of these flowers. The process which occurs in the umbel of *Siler* is but slightly different, although the flowers are exclusively protandrous, and not protogynous like those of *Pachypleurum*. In spite of this difference in the times of maturation the end attained is the same, as we shall see. The flowers in an umbel of *Siler* do not mature simultaneously like those of *Pachypleurum*, but the development proceeds very gradually from the circumference towards the centre of the umbel, so that the anthers of the central flowers do not dehisce until the outer ones have lost their pollen and matured their stigmas. Some of the crumbling pollen which falls out of the shrivelling anthers is now deposited on these ripening stigmas, since the thread-like filaments are long enough to reach to the middle of the outer flowers, and thus geitonogamy almost invariably ensues.

Both *Pachypleurum* and *Siler* and all the Umbelliferæ typified by them contain only hermaphrodite flowers in their umbels, and in this respect they differ from species of *Athamanta*, Spignel (*Meum*), and Chervil (*Chærophyllum*, see figs. 294^3 and 294^4, p. 320), whose umbels contain both hermaphrodite and staminate flowers like those of *Astrantia* and *Sanicula*. But this arrangement of the flowers causes no alteration in the process of fertilization described. We would merely observe that in these plants the hermaphrodite flowers always open earlier than the staminate flowers of the same umbel. Not until the stamens of the hermaphrodite flowers have dehisced and fallen away, whilst their stigmas have been waiting for two days for pollen from other plants, do the anthers of the staminate flowers open after growing up far beyond their corollas. Their pollen then falls on the stigmas of the hermaphrodite flowers. Since there are so many more staminate than hermaphrodite flowers, the success of the process is doubly assured. For example, the umbel of *Chærophyllum aromaticum* (see figs. 294 [3] and 294 [4]) contains 20 staminate flowers besides one central and 3-5 peripheral hermaphrodite flowers, and therefore to 8-12 functional stigmas there are about 100 anthers. Moreover, the hermaphrodite flowers in these Umbelliferæ assume such a position at the moment the staminate flowers open that a pollination of their stigmas by the falling pollen is almost unavoidable (fig. 294 [4]).

One of the most remarkable instances of geitonogamy is observed in such Umbelliferæ as the Beaked Parsley (*Anthriscus*), Fennel (*Fœniculum*), Coriander (*Coriandrum*), Water Parsnip (*Sium*), and *Ferulago*. All the species of these genera have two kinds of inflorescence. The umbels which blossom first contain principally true hermaphrodite flowers with a few isolated staminate flowers here and there; the later umbels consist only of staminate flowers. The hermaphrodite flowers which come first are completely protandrous; the anthers, borne on very thin filaments, are brought one after the other to the centre of the flower, where they dehisce and scatter their pollen, and the day following they drop off. After all the five stamens have dropped off the stigmas become mature and receptive. They continue in this condition for two days, and during this period are liable to crossing with the pollen of other plants. Then the umbels bearing only staminate flowers come under consideration. The pedicels which bear them have meanwhile elongated, and have thus obtained such a position that these umbels stand right over the hermaphrodite flowers with their mature stigmas, so that they seem to form an upper story, so to speak, in the inflorescence as a whole. Now, when the anthers in the staminate flowers of this upper story open, and when their walls shrivel up, the pollen is thrown out and falls vertically downwards in minute crumbling masses. The stigmas of the lower, older flowers are thus subjected to a rain of pollen, and it is easy to see that the majority of the stigmas are pollinated in this manner.

The instances of geitonogamy described in Compositæ and Umbelliferæ may be regarded as typical of what occurs in many representatives of other families. The Stellatæ section of Rubiaceæ, Caprifoliaceæ, Cornaceæ, Scrophulariaceæ, Rosaceæ, Polygonaceæ, Liliaceæ, and Aroideæ, whose flowers are crowded together in capitula, balls, fascicles, spikes, and racemes, repeat these processes sometimes down to the minutest detail. For example, the two styles in the protandrous fascicled flowers of a Woodruff, *Asperula taurina*, elongate, separate from each other and bend over just like those of *Laserpitium*; by this alteration of position they get into the region of the younger flowers, where pollen is being shed, and their stigmas thus actually come into contact with the pollen. The process is still further promoted in this species of Woodruff by the fact that the last flowers to be produced are staminate. In the Red-berried Elder (*Sambucus racemosa*), various species of the Cornel and Dogwood genus (*Cornus florida, mas, sanguinea*), in the Vines (*Vitis*), which bear true hermaphrodite flowers, in the Tufted Loosestrife (*Lysimachia thyrsiflora*), and in many Spiræas (*Spiræa*), the arrangements for geitonogamy resemble those of *Siler trilobum* in that the direction of the style and the position of the stigma remain unaltered, but the filaments of the anthers elongate and bend over so as to deposit the pollen on the stigmas of adjacent flowers. In the Wayfaring-tree and Guelder-rose (*Viburnum Lantana, V. Opulus*) we have yet another contrivance—the pollen which is shed from the bent anthers of one flower falls to the bottom of the cup-shaped corolla of an adjacent one, where the large cushion-like stigma is situated.

The process of geitonogamy in the Snake-root (*Calla palustris*) and in *Saxifraga juniperifolia* to some extent resembles the fall of pollen in Compositæ. The flowers in these plants are crowded in short spikes or fascicles. They are protogynous, the stigma in the lower half of the inflorescence not ripening until the upper flowers are shedding their pollen. Now, when the anthers begin to shrivel and the pollen is thrown out, it necessarily falls on the fertile stigmas below. In those species of *Veronica* which have spicate inflorescences (*Veronica maritima, spicata, spuria*, &c.), the method of geitonogamy is slightly different, for here the style undergoes peculiar movements during the flowering period. The crowded flowers are all protogynous, and the stigmas of the flowers which first unfold are exposed to the pollen of plants of other species. This continues for two days. Meanwhile the stamens of the lowest flowers on the spike have elongated and pushed their anthers into the place first occupied by their stigmas; the anthers then dehisce and shed their pollen. But shortly before this the style has bent sharply downwards so that it is impossible for its stigmas to come in contact with this liberated pollen. Not until all the pollen has fallen down by the shrivelling up of the anthers or has been carried away by insects do the styles again straighten and project almost horizontally from the axis of the spike. The upper flowers on the spike undergo the same course of development, but the stages here are two days later. On this account the pollen falls from the anthers of the higher flowers just when the styles of the lower flowers again become straight. The still fresh stigmas at the ends of the styles thus come into line with the falling pollen and are efficiently pollinated by it.

A similar process occurs in *Eremurus* (see fig. 293 ^{2}, p. 309), but here there is no fall of pollen. The stigmas at the end of the just straightened style are brought by their change of position directly into contact with the orange-yellow pollen still clinging to the withered anthers of the higher flowers. Many of the styles, of course, brush by the anthers without effecting this contact, and accordingly many stigmas in the racemes of *Eremurus* remain unpollinated. The transfer of the pollen by insects occurs but seldom in this plant, so that from the many ovaries in the inflorescence of *Eremurus* usually only a few fruits are matured. This is the more remarkable as these flowers have remarkably long-lived stigmas, a peculiarity which is generally very advantageous in bringing about cross-pollination. The stigma is already mature when the perianth opens; when the tips of the perianth roll back and assume the form of aphides (see p. 171), and when the style moves like the hand of a watch towards the axis of the inflorescence, the stigma is still receptive, and remains so even when the style has again straightened and assumed an oblique upward direction.

A peculiar instance of geitonogamy is observed in *Allium Victorialis*. Each umbel is composed of flowers of very different ages. Before the first flowers bend over, wither, and shrivel up, their pollen-covered anthers project well over the edge of the perianth. In the younger flowers, at the same time, the anthers are still closed and covered by the perianth-leaves, but the stigmas are ripe and project beyond them. These young and hitherto short-stalked flowers are now raised by the elongation of their pedicels and inserted between the older flowers, so that, as a matter of course, their stigmas are brushed by the pollen of the older flowers, if it does not indeed fall on them.

The geitonogamy in the Bistort (*Polygonum Bistorta*) is very strange. It is rendered rather complex, as a peculiar distribution of the sexes is combined with a pronounced dichogamy and a peculiar way of opening. The inflorescence, which looks like a spike, is really composed of numbers of tiny two-flowered groups crowded together. One of the two flowers of each little group is long-styled and truly hermaphrodite, while the other contains a short style, well-formed stamens, and a rudimentary ovary which develops no further. It is therefore a pseudo-hermaphrodite staminate flower. In each group the long-styled hermaphrodite flower opens first, beginning at the base of the apparent spike and gradually working up to the top. The staminate flowers do not get their turn until the highest of the long-styled flowers has opened; but after this they behave exactly like their neighbours, *i.e.* the lowest develops first. The long-styled flowers are protandrous. At the commencement of flowering the pollen-covered anthers project a millimetre from the perianth; the styles, however, are still short and hidden in the interior. At this time pollen can only be removed from the flowers. Then the anthers fall off and the styles elongate so as to protrude some 3 mm. beyond the perianth. The whole spike is at this stage beset with receptive stigmas which can only be fertilized by insects with pollen from other plants. But this state of things does not last long, for now the staminate flowers open one after another in quick succession. Their anthers, containing abundance of pollen, protrude 3 mm. beyond the perianth and come into contact with the still receptive stigmas of their neighbours, so that geitonogamy results. As soon as this is effected the staminate flowers become detached from the axis of the spike and fall to the ground. This geitonogamy is of course useless to the stigmas which have already received pollen from other plants by insect agency, but it is of the greatest importance to the flowers which have not been so visited, for they would otherwise wither without being pollinated. In this sense we may regard the staminate flowers of *Polygonum Bistorta* as reserve flowers which, in case of absence of insect-visits, can come to the rescue in the last extremity with their own pollen.

Many plants related to the Bistort belonging to the Rhubarb and Dock genera (*Rheum, Rumex*), and many species of the Meadow-rue (*Thalictrum*) belonging to the Ranunculaceæ, agree for the most part with the case just described. The hermaphrodite flowers of the Rhubarb are protandrous. The anthers project, one after the other, above the edge of the tiny bell-shaped perianth, where they open and emit their floury pollen. This is easily shaken off by the least movement, and soon afterwards the anthers tumble off their filaments. At this time the three styles on the top of the ovary are bent back, and the large, swollen, cauliflower-like stigmas are so hidden at the base of the perianth that the pollen can gain no access to them. Not until all the anthers have fallen off do the styles straighten and place their succulent three-lobed stigmas in front of the edge of the perianth. Since the development of the extensive inflorescences of the Rhubarb takes place only gradually, one flower withering when another near it has just opened, the pollen shaken from the anthers of the younger flowers usually falls on the stigmas of the older ones. Sometimes the pseudo-hermaphrodite staminate flowers, which also occur in the inflorescence of the Rhubarb, and which are the last to open, have to provide the pollen for the adjoining hermaphrodite flowers, and after having performed their task they fall off. The course of development in the Alpine Dock (*Rumex alpinus*) gives rise to geitonogamy, but the process differs from that in the Rhubarb, since the stigmas do not emerge from their hiding-place in the depths of the perianth by the straightening of the style, but are rendered conspicuous by the folding back of the perianth-leaves, whilst in several Meadow-rues (*Thalictrum alpinum, fœtidum,* and *minus*) the stigmas, which are at first concealed under the petaline sepals, are exposed and rendered accessible to the pollen of neighbouring flowers by the falling away of the sepals which cover them.

These plants have floury pollen which, in the absence of wind, may fall vertically on the stigmas of neighbouring flowers, but whose transport is usually effected by breezes. They therefore afford a transition to such plants as have hermaphrodite flowers in which geitonogamy is chiefly brought about by the wind, although it may also result in the same way as in the Meadow-rues and the Docks and Rhubarbs. These plants were mentioned when we were considering the inadvisability of dividing plants into those which are respectively anemophilous and entomophilous (see p. 129). These plants would belong to both classes; at first they are insect-fertilized, and later on they are fertilized by the wind. The Mediterranean Heath (*Erica carnea*), which grows in Alpine districts from the valley-floor almost to the summits of limestone mountains, may be taken as the type of some two hundred Ericaceæ. This plant is much frequented by bees, and their visits are the cause of manifold crossings, sometimes between the flowers of the same plant, sometimes with other plants. In this plant, however, the crossing of neighbouring flowers is more often effected by the wind. This process will be rendered clearer with the help of figs. 295[1, 2, 3, 4]. The flowers are arranged in a row, with their mouths directed to one side pointing obliquely downwards (295[1]). Flowering begins at the top of the branch, and then works gradually downwards. The stigma comes into sight simultaneously with the opening of the corolla, and protrudes some distance in front of its mouth by the elongation of the style. The anthers surrounding the style are still closed, and are either wholly or half hidden in the corolla (295[2]). Bees coming to suck the honey at the base of the flower inevitably brush against the stigma in consequence of its peculiar position. If they have brought pollen with them from other Heaths, a crossing between different plants is the result. Meanwhile large pores have formed in the anthers (see fig. 295[4]). But since the pores on adjacent anthers are in immediate contact with one another, and since the anthers themselves are held together by the corolla (which is rather constricted at its mouth), as if by a ring, the pollen remains stored up in the anther-cavities and the pollen-tetrads do not fall out unless disturbed in some way. The anthers are disturbed whenever a bee inserts its proboscis into the flower in search of the honey, and therefore the same bee which at first brushed against the project-

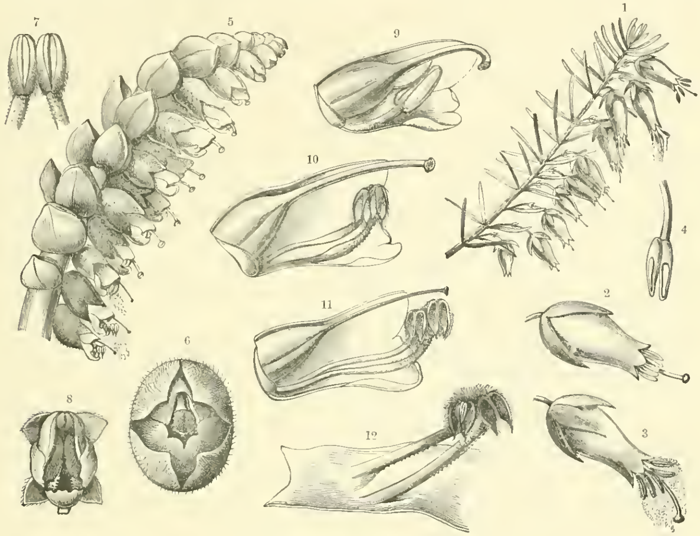


Fig. 295.—Geitonogamy with dust-like pollen.

[1] *Erica carnea*; branch with flowers on one side only. [2] Flower of the same in its first stage. [3] The same flower in its last stage. [4] Single stamen of *Erica carnea*. [5] *Lathræa Squamaria*; upper part of inflorescence. [6] Front view of a flower which has just opened. [7] Two anthers with closed loculi from the same flower. [8] Front view of a flower at a later stage. [9, 10, 11] Longitudinal sections of three flowers in the first, second, and third stages respectively. [12] Two anthers whose floury pollen has fallen, leaving empty loculi. [1] and [5] nat. size; the others somewhat enlarged.

ing stigma is, in the next instant, smothered in pollen over its proboscis, head, and thorax. Cross-pollination must ensue if this bee shortly after visits the flowers of another plant, and wherever Heaths which flower simultaneously grow together there is no lack of hybridization. Whether the stigma of a flower is pollinated by bees with pollen of another plant of the same or of another species or not at all, it always begins to wither in two days' time and ceases to be receptive. The stamens in the same flower now elongate and push their anthers out of the corolla mouth. The restriction being removed the anthers separate, and pollen will fall out of their compartments at the slightest movement (see fig. 295 ³). The merest swaying of the flowering branch is sufficient to cause the pollen to fall. The still receptive sticky stigmas of the younger flowers on the same branch, and indeed of flowers on other branches of the same plant at some distance, are thus necessarily pollinated with the dust-like pollen.

In the inflorescence of the Toothwort (*Lathræa Squamaria*) the crossing is effected in exactly the same way. The flowers, like those of the Heath, are all turned towards the side from which insects may be expected to arrive (see fig. 295 ⁵). They are protogynous, and the ripe stigma projects beyond the margin of the corolla before the latter has properly opened and when the anthers below are still closed (see figs. 295 ⁶, ⁷, ⁹). At this stage the stigma can only be pollinated with the pollen of other plants whose development is further advanced. Corolla, style, and filaments continue to elongate, the style, which has hitherto been bent like a hook, straightens, the stigma, which was formerly in front of the narrow entrance to the flower, takes a higher position, the anthers dehisce, and the flower now enters upon its second stage (see figs. 295 ⁸ and 295 ¹⁰). Pollination is effected at this time by insects. Humble-bees suck the honey secreted by a succulent cushion below the ovary, and so transfer the pollen of the Toothwort from flower to flower. When they come to a flower they brush against the projecting stigma and deposit pollen on it which they have gathered elsewhere; they then push their probosces between the anthers, which are held together by soft hairs. They are obliged to take this path, for otherwise they would soon come to grief. The filaments below the anthers are studded with little pointed thorns (see fig. 295 ¹⁰), and the humble-bee carefully avoids any contact with them. He therefore passes between the contiguous anthers of the sprinkling stamens (*cf.* p. 271), separating them slightly, and thus causing a fall of dusty pollen which covers his proboscis and head. And now comes the third and last stage. The style and stigma wither and dry up, and the stamens elongate and push their anthers beyond the margin of the corolla (see figs. 295 ¹¹ and 295 ¹²). The anthers no longer cohere. The pollen retained in their cavities is carried away by the wind, and will be deposited in part on the still receptive stigmas of neighbouring, younger flowers. If a flower has already been visited by a humble-bee very little pollen will remain in its anthers, but if there has been no insect-visit the anthers are full of pollen when they are extended from the flower, and this is wafted in small clouds to the stigmas of the younger flowers in the upper part of the spike. Here again, as in so many instances, geitonogamy does not supervene till towards the close of flowering. At first the plant seems to offer facilities for hybridization, later for a crossing of different plants of the same species, and not until both these processes have failed, owing to lack of insect-visits, does it fall back on cross-pollination between neighbouring flowers of the same plant. The processes and contrivances in the flowers of *Clandestina rectiflora*, *Bartsia alpina* and of some other Rhinanthaceæ agree in the main with those of the Toothwort, so that there is no need to describe them in detail. In conclusion, the Persian *Crucianella stylosa*, one of the Stellatæ group of the Rubiaceæ, must be considered especially with regard to the geitonogamy of its hermaphrodite flowers. This plant has already been mentioned (pp. 265, 267), and it was stated that the tips of the corolla-lobes formed a hollow cone which at a touch suddenly burst open, scattering the pollen hidden beneath (fig. 272). If an insect is the cause of the disturbance it becomes covered with the liberated pollen, and should it then visit other flowers of this same *Crucianella* it is not too much to say that the pollen it carries on its body will be deposited on the stigmatic tissue at the thickened end of the slender styles projecting far above the corolla (see fig. 272 ^{5}). If the flower is not visited, however, it will burst open and scatter its pollen spontaneously. The dust-like pollen is then diffused into the surrounding air, and so easily reaches the ripe stigmas of the neighbouring flowers.

AUTOGAMY.

By the term *Autogamy* is understood the transference of pollen from the stamens to the stigmas of the same flower, in other words—*self-pollination*. Autogamy can, therefore, only occur in hermaphrodite flowers, but it must not be inferred that the only method of reproduction in hermaphrodite flowers is by autogamy. In the last chapter we showed the error into which Linnæus fell by making this assumption, and referred to the almost interminable list of contrivances to bring about cross-pollination in hermaphrodite flowers between different species, between different individuals of the same species, and between flowers on the same individual. This important result of modern investigation has led not only to a correction of the views of the celebrated Swedish Botanist, but to the belief that autogamy is avoided in the vegetable world. Darwin even held the opinion that there must be something injurious in autogamy to account for the number of obstacles placed in its way. This statement, though commonly made in text-books as embodying a law of nature, is, however, not a correct expression of the facts observed. It is true that cross-pollination appears to be the primary object aimed at, but it is not true that autogamy is avoided. If cross-pollination takes place there is naturally no necessity for subsequent autogamy, but if cross-pollination fails autogamy assumes an importance of its own, and the contrivances which have been observed to bring about autogamy are no less numerous than those which favour cross-pollination. That flowers should be adapted at different times to two such diverse purposes as cross- and self-pollination is one of the marvels of floral construction.

As the above conclusion forms the main basis of the theory concerning the origin of species to be presently unfolded, some preliminary account of the observations on which it is founded must now be given, but the task is not an easy one. For five-and-twenty years I have been studying, with special reference to the phenomena in question, the flowers of many more than a thousand species in all stages of development from budding to fruiting, some growing wild in their original habitats, some in the Gardens under my direction, and my notes are so numerous that even the briefest outline of the cases observed would fill several volumes. I must, therefore, content myself with presenting the different instances in groups according to their degrees of similarity. Even the number of groups, however, is surprisingly large, and only their general description can be attempted. The best way will be to select a representative species for each kind of adaptation that we have to deal with, and to point out in a few words its more important characteristics. As the processes to be described as taking place during the flowering period all tend to the same result though differing greatly in other ways, and as the terms used must be applied over and over again to the phenomena which are common to all the cases, it is impossible to avoid a certain monotony in the descriptions that follow, and the reader is begged to exercise some patience in the perusal of this chapter.

The simplest case of autogamy occurs as follows. The flower opens revealing the stigma stationed in front of the entrance to the receptacle and already mature, whilst the anthers are closely adherent to the stigma but are still closed. Autogamy is, for the time, impossible, whereas cross-pollination may be effected through the intervention of wind or insects. In the second half of the flowering-period the anthers adjacent to the stigma open, and the stigma is instantly covered with the pollen set free from them. There are only a few varieties of this simplest case of autogamy worth mentioning. It has been observed to occur in particular in annual plants with small flowers (e.g. *Centunculus minimus*, *Geranium pusillum*, *Lithospermum arvense*), and again in several bulbous plants belonging to the section of LiliflorEæ, *e.g.* several species of *Fritillaria* and *Narcissus*, all the species of *Trillium* and *Uvularia*, and in a few species of *Crocus*. In *Trillium grandiflorum* and *Uvularia grandiflora*, two anthers are stationed in each of the three angles of the spreading stigmas, and in the process of autogamy only the pollen from that half of the anther which is turned inwards is used, whilst the pollen from the outward-facing halves of the anthers may be carried away by insects, even after autogamy has taken place. In the Crown Imperial (*Fritillaria imperialis*) only the pollen from the three longer stamens falls upon the stigma of the same flower. There are six stamens in the flowers of this plant, three of which are longer than the rest and alone have their anthers appressed to the tridentate stigma. These anthers open a day later than the others. Dehiscence is accompanied by a very considerable shrivelling and shortening of the anthers, and the result of this contraction is that the liberated pollen is scraped off the anthers by the edges of the stigmatic lobes. In *Crocus albiflorus*, which covers alpine meadows in early spring with its blossoms, the anthers at first rest with their arched backs in contact with the stigma. The loculi, full of adhesive pollen, face outwards, and are so placed that insects coming in quest of honey must rub off the pollen emerging from their slits. The stigmas, on the other hand, assume such a position that the insects are obliged to touch their receptive tissue before brushing the anthers. Owing to the relative positions of stigmas and anthers cross-pollination is no doubt effected by insects in a large number of cases, and as only the backs of the anthers rest upon the stigma autogamy is, for the time, impossible. But towards the close of the flowering period the anthers are twisted round, with the result that the pollen of each loculus touches the stigma. Another circumstance contributory to this autogamy is that during the time of flowering the perianth-tube elongates from 5 to 15 mm., and the filaments, which are adnate to the perianth, from 3 to 4 mm. The anthers are in consequence pushed past the stigmatic margins and leave more pollen upon them than would otherwise be the case.

Convolvulus Siculus, a native of the shores of the Mediterranean, may be taken as a type of several annual Bindweeds wherein the style bifurcates into two narrow filiform branches of considerable length which bear the receptive tissue and represent stigmas. One of these stigmas is erect, and continues the style in a straight line, whilst the other stands away at an angle of 60°, and forms a barrier in front of the approach to the floral receptacle. The stamens are adherent to the style, and at the time that the corolla opens the anthers rest against the erect stigma. At the period of dehiscence the anthers face outwards so that the upright stigma encompassed by them cannot receive their pollen when the flower first opens. On the other hand, the position of the anthers is favourable to the abstraction of pollen by insects seeking the honey in the interior of the flower. Later on, when the anthers shrivel they become covered all over with pollen, and then it is that a portion of it is transferred to the erect stigma, thus effecting autogamy. The second stigma, which lies across the entrance, seldom has pollen from the anthers of the same flower affixed to it; but pollen conveyed from other flowers is rubbed off insects on to this stigma, so that here we have an instance in which one stigma is adapted to autogamy and another to cross-pollination.

The process of autogamy occurs in pendent flowers, the anthers of which are joined together in a central cone, through a relaxation of the filaments towards the close of the flowering period, in consequence of which the loculi full of pollen no longer close together so tightly as before. The mealy pollen falls from the dislocated cone upon the stigma, which is still in a viscid and receptive condition. As types of this category of plants we may take the Snowdrop (*Galanthus*), *Soldanella*, of which previous mention has been made (see fig. 278 [1], p. 275), and *Dodecatheon*, which is allied to *Soldanella*, but in respect of the form of its flowers resembles *Cyclamen*. During the first part of their flowering-period they are adapted to cross-fertilization. The style projects far beyond the cone of anthers. Insects in search of honey begin by brushing against the stigma and then for a moment dislocate the anthers, letting a sprinkling of pollen fall on their heads. On visiting other flowers they rub this pollen on to the stigmas and so promote cross-fertilization. If, however, no insects visit a flower, the anthers are still full of pollen at the close of its flowering period, and being then displaced let fall their pollen upon the slightest vibration of the pendent blossom, or even when it is quite still. The pollen falls straight down and is caught by the stigma below.

The process above described is only observed to take place in pendent flowers where the pollen is of floury consistency and the stamens are united into a conical cap. Flowers borne on horizontal stalks, and facing sideways, may exhibit the same phenomenon in connection with separate stamens. Only an important circumstance in this case is that some of the anthers should be exactly over the stigmas at the time of dehiscence. With a view to cross-fertilization, lateral flowers of the kind are protogynous, and have their anthers closed when the buds open; but later on the anthers dehisce, and a portion of the pollen then liberated falls out, owing to the contraction of the walls of the anthers, and besprinkles the stigma of the same flower. This method of autogamy has been observed in particular in the flowers of *Tofieldia* and the Bog Asphodel (*Narthecium*).

Even in upright flowers autogamy sometimes takes place in the second half of their time of flowering through a fall of pollen, and that without any change of position on the part of petals, stamens, or style. To make cross-fertilization possible, in the first instance, flowers of this kind are protogynous. Subsequently, after the dehiscence of the anthers, a portion of the crumbly pollen becomes detached, and is deposited on the stigma below. In the case of erect flowers with funnel-shaped corollas, the pollen slips down the smooth sloping wall of the funnel to the stigma, and it is not essential for the anthers to stand vertically above the stigma, since the corolla acts as a sort of conduit for the pollen. The Lilac (*Syringa*) is an example of the plants of this category. It is also remarkable for the fact that, though its flowers are only protogynous for a very short time, yet, for one or two days after the dehiscence of the anthers, autogamy cannot take place, because the anthers face outwards. So long as the anthers are in this position the pollen cannot be transferred without extraneous aid to the corolla-tube; it is not till later on, when the anthers get covered all round with pollen, owing to the gradual shrinkage of their walls, that some of the pollen drops on to the stigma standing underneath in the tube of the funnel.

Very often in erect or obliquely ascending flowers autogamy is brought about by an elongation of the filaments during the period of flowering, the result being that the anthers, which are originally lower down than the stigmas, are elevated to the same level as the latter, and are thus enabled to deposit their pollen upon them. Most of the species belonging to this group are protogynous; the filaments are erect, and are either adherent or else parallel to the ovary or style. At first the anthers are so far from the stigma that the pollen would not of itself dust the stigma in the same flower, but the subsequent elongation of the filaments is so regulated as to carry the anthers to the same level as the stigma by the time they are coated with pollen. The anthers then adhere to the receptive stigmatic tissue, and autogamy is the result. The following are instances of plants in which this is observed to occur:—the Moschatel (*Adoxa Moschatellina*), most of the species of the Knawel (*Scleranthus*), *Pæderota Bonarota*, of wide distribution in the Southern Alps, the curious *Aponogeton distachyon*, native to South Africa, and a large number of Cruciferæ, Saxifragaceæ, Willow-herbs, Geraniaceæ, Convolvulaceæ, and Caryophyllaceæ.

Of the large family of the Cruciferæ we may mention *Arabis cærulea*, *Braya alpina*, *Cardamine alpina*, and *Rhizobotrya alpina*, all of which are small-flowered species growing in the upland hollows of high mountains, and in addition the annual or biennial species named *Lepidium campestre*, *L. sativum*, *Sisymbrium Alliaria*, *S. Thalianum*, *Thlaspi alliaceum* and *Thlaspi arvense*. In these plants the stigma is sessile on the ovary in the shape of a small round cushion, which becomes visible the moment the imbricate petals of the bud begin to move apart. At this period only cross-pollination can take place, as all the anthers in the flower itself are still closed; but the four long stamens now grow up along the wall of the ovary until the anthers are exactly on the same level as the stigma. The anthers have dehisced by that time, and their pollen cannot but be deposited on the receptive cells at the periphery of the stigmatic cushion. Another observation which has been repeatedly confirmed, is that only one of the four anthers parts with its pollen to the adjacent stigma, while the rest, though quite close to the stigma, are not in immediate contact with it. The pollen of these three anthers is apparently placed there so that it may be carried off by the small flies which visit these cruciferous plants and transferred by them to younger blossoms.

The Saxifrages (e.g. *Saxifraga androsacea*) here in question have two linear or oblong stigmas. After the anthers are raised, the pollen is usually brushed off them on to the sides of the stigma near its base. But here again it is noteworthy that for the most part only one of the five anthers devotes its pollen to the process of autogamy, whilst the others remain a little below the stigmas, and do not come into contact with them.

In a number of small-flowered Willow-herbs (*Epilobium collinum*, *E. montanum*, *E. parviflorum*, &c.) the stigma is composed of four thickish divergent lobes arranged in a cross with four angles between them. Upon the first parting of the petals, which always happens early in the morning, the anthers may be seen to be underneath the mature cruciform stigma, but in the course of that very day the filiform filaments grow to a sufficient length to place the anthers in the re-entrant angles of the cross. Meanwhile, dehiscence has taken place, and by the evening of the first day autogamy ensues. During the night the petals close up, and the flower droops a little; the next morning the petals open again, and it is then evident that the filaments have grown rather longer, two or three pollen-covered anthers standing above the stigma and partially concealing it. The place occupied by the stigma on the previous day is now filled by an assemblage of anthers laden with pollen, which is brushed off by insects and transported to other flowers. Thus we find in these Willow-herbs that on the first morning cross-fertilization alone is possible, in the evening of the first day autogamy takes place, and on the next day pollen is again supplied to fertilize younger flowers—an alternation which clearly shows that autogamy is not invariably merely a last stage in the phenomenon of flowering.

Similar events occur in several small-flowered species of the Crane's Bill (e.g. *Geranium columbinum, G. lucidum, G. Robertianum*). In the middle of the newly-opened flower is a receptive stigma with five radiating arms, and around it are ten stamens, all of which are still closed. Five of the stamens are longer than the rest, and hold their anthers nearly on a level with the stigma; the other five anthers form a belt underneath the stigma. By the evening of the first day the anthers of the longer stamens are already open, and transfer their pollen to the tips of the adjacent stigmatic lobes. In *Geranium lucidum* the phenomenon is not even delayed till the evening, but takes place four hours after the flowers open. The flowers are not, however, then over. They close for the night, and nod or droop to protect the pollen (see figs. 225^1 and 225^2, p. 121), but next morning they again become erect. The five stamens standing in front of the petals then grow until the anthers reach the niches between the radiating lobes of the stigma, whereupon there is a transference of pollen to these lobes. Some of the anthers are afterwards lifted still higher, evidently for the purpose of dispersing, by aid of insects, such portion of the pollen as has not been applied to the process of autogamy.

Several Convolvulaceæ, of which the well-known *Ipomœa purpurea* is a type, have only two or three of their five stamens adapted to autogamy. The stamens, which are parallel to the style and usually adherent to it, are of unequal length, the shortest being 9 mm., the longest 17 mm., and the others 11 mm., 13 mm., and 15 mm. in length respectively. The anthers consequently stand at different heights and at the same time they are so disposed relatively as not to cover one another, an arrangement which has the advantage of presenting a comparatively large expanse of pollen along the passage leading to the honey in the interior of the flower. But even the anther of the longest stamen is 3 mm. lower than the stigma when the flower first opens. Owing to this arrangement and to the circumstance that the flowers are protogynous, only cross-fertilization through the intervention of insects can take place at the commencement of their flowering period. Later on, however, there is a lengthening of the stamens and the anthers pertaining to the longest two or three reach the same level as the stigma, and yield up their pollen to it. The process of autogamy is further facilitated by the involution of the corolla, which occurs at the close of flowering, whereby the anthers coated with pollen are pressed against the stigma.

From these Convolvulaceæ we pass to a long series of protandrous Caryophyllaceæ, mostly annual plants, such as *Agrostemma Githago, Saponaria Vaccaria*, and *Silene conica*, in which the anthers are brought into contact with the stigmas by a similar elongation of the stamens. The various changes occurring in flowers of the kind ensue with great regularity as follows:—(1) The petals separate, leaving the approach to the floral receptacle open. Dehiscence has already taken place in the case of the anthers of the stamens inserted in front of the sepals, and their pollen is available for cross-fertilization by means of insects, but not for autogamy, owing to the fact that the receptive tissue of the style in the same flower is still inaccessible. (2) The anthers of the stamens inserted in front of the sepals drop off, or else their filaments become reflexed and are exserted beyond the periphery of the flower. The styles move asunder and arrange themselves like the spokes of a wheel in the middle of the flower, where they are liable to be covered with pollen brought by insects from other blossoms. The anthers of the stamens inserted in front of the petals are still closed. (3) Owing to a growth of the erect filaments of the last-mentioned stamens, their anthers are brought to the same height as and in direct contact with the spreading stigmas. Dehiscence ensues, and the liberated pollen is deposited on the receptive stigmatic tissue. In annual caryophyllaceous plants—*e.g.* in *Silene conica*—the whole process takes place in the course of a single day, whereas in the perennial *Dianthus glacialis* it occupies five or six days, or, if the weather is bad, from seven to nine days.

One of the commonest contrivances for effecting autogamy is the following. Anthers and stigmas stand at the same height, though, owing to the position and direction of the filaments, the anthers are so far from the stigma that no transference of the adhesive pollen to it can take place. At the proper moment, however, the straight and rigid filiform filaments perform certain special movements with the object of conveying pollen from the anthers to the stigma in the same flower. The filaments incline themselves towards the centre of the flower, bringing the anthers into contact with the stigma there situated and pressing the pollen issuing from their loculi on to the receptive tissue. In some plants belonging to this category the displacement of the stamens, which is like the motion of the hands of a clock, is preceded by an elongation of the filaments, and in this respect the plants in question form a transition from those previously described, in the flowers of which autogamy is due to the growth of the filaments. As instances of these transitional forms may be mentioned *Azalea procumbens, Draba aizoides, Haplophyllum Biebersteinii*, the numerous Saxifrages comprised in the groups of Aizoonia and Tridactylites, and more particularly many Alsineæ and other Caryophyllaceæ. The Saxifrages exhibit a number of individual peculiarities into which we cannot enter in any detail. We must content ourselves with describing two species as representatives of the two groups above referred to, and will select for the purpose *Saxifraga Burseriana*, a plant which grows in the eastern Dolomites, and flowers in early spring, and *Saxifraga controversa* of the group Tridactylites. The flowers of *Saxifraga Burseriana* are protogynous, and the two spreading stigmas are already susceptible of pollination at the time when the petals are only just open, and the anthers are still closed and held near the bottom of the flower on quite short filaments. During this first period of flowering the blossom is adapted to cross-fertilization. Soon afterwards the stamens in front of the sepals lengthen in definite succession, and the anthers, which meanwhile have undergone dehiscence, are brought to the same level as the stigma. Although the horizontal distance between the stigma and anthers is very small, it is still sufficient to prevent the stigma from becoming coated with pollen from the anthers. Moreover, the stamens standing opposite the sepals incline outwards soon after, thus increasing perceptibly the distance between anthers and stigma. Synchronously with the outward inclination of these stamens there is an up-growth of those which stand in front of the petals, and here again the operation takes place according to a definite law of succession, and continues until the anthers are raised to the height of the stigmas. These anthers, like the others, do not adhere at first to the stigma, and it sometimes happens that the stigma remains unsupplied with pollen even on the sixth day of flowering if none is brought by insects. But, at last, on the seventh or eighth day some, if not all, the filaments move towards the centre of the flower, and the pollen-covered anthers are pressed against the stigma, which has not yet lost the power of receiving the pollen. Usually the five stamens opposite the sepals act in the same manner, and all the ten anthers then ultimately form a ring surrounding the stigma from which pollen may still be transferred by insects to other flowers. The flowers of *Saxifraga controversa* are likewise protogynous, and adapted to cross-fertilization in the first period of flowering. Of the ten stamens, the first to elongate are the five opposite the sepals; the anthers borne at their extremities ascend to the level of the stigma and during the process accomplish their dehiscence. For a short time anthers and stigmas are separated by a small interval of space, but soon afterwards the filaments incline a little towards the centre and deposit pollen upon the stigmas. The five stamens in question then slope away from the centre, and their empty and shrivelled anthers fall off. Meanwhile the five stamens opposite the petals have grown up to the level of the stigmas and offer a fresh supply of pollen for dispersion. But this pollen cannot be used for autogamy owing to the fact that the stigmas shrivel up after they receive the pollen of the first five stamens, and are no longer capable of playing a part in fertilization. The second supply of pollen can, therefore, only be appropriated to the fertilization of younger flowers through the instrumentality of insects. In other words, the five anthers in front of the sepals devote their pollen to autogamy, whilst the five opposite the petals devote theirs to cross-fertilization.

As in these Saxifrages so also in Alsineæ we find two whorls of stamens opposite the sepals and petals respectively, and a certain general resemblance unmistakably exists in the whole arrangement of the various parts of the flowers. The Alsineæ that we here have to deal with are protandrous, and as examples may be taken *Cerastium longirostre, Malachium aquaticum, Sagina saxatilis, Spergula arvensis,* and *Stellaria media*. Dehiscence takes place in the anthers opposite the sepals synchronously with the opening of the corolla, and the pollen exposed thereby is available for cross-fertilization. At that period the styles are still coherent, and the stigmatic tissue, which is composed of short transparent hairs, is inaccessible. Soon afterwards, however, the styles part asunder, and the stigmatic tissue assumes such a position as to ensure cross-fertilization in case insects bringing pollen from other flowers should visit them in quest of honey. In a short time the stamens opposite the petals raise their anthers to the same height as the stigmatic tissue of the divergent styles; but the filiform filaments slope away from the axis, so that there is always some interval, however small it may be, between anthers and stigmas, and there is still no autogamy. It is not till the last moment, when the flowers begin to close, that the stamens opposite the petals incline towards the centre of the flower, and, laying their anthers upon the stigmatic tissue, cover it with a quantity of their still abundant store of pollen. In most of the Alsineæ, of which we are speaking, the anthers in front of the sepals also come into contact with the stigmas at the same moment, but in a few cases they project above the stigmas and petals, and their pollen is then not available for autogamy. It is remarkable that in the the latter, which may be represented by *Sagina saxatilis*, the characteristic fact of the pollen of the five stamens opposite the sepals being devoted to cross-fertilization, and that of the five stamens opposite the petals to autogamy, is exactly the reverse of the arrangement found to exist in the Saxifrages above described.

Next to this series of plants of which the Saxifrages of the Aizoonia and Tridactylites groups and the Alsineæ above-named are the chief representatives, comes another composed predominantly of Cruciferæ. They are for the most part annual species with small flowers, which are but little visited by insects, and the majority of their fruits must be looked upon as products of autogamy. *Cochlearia Greenlandica, Draba borealis, Draba verna, Clypeola Messanensis, Lobularia nummularia, Hutchinsia alpina, Schieverekia Podolica, Lepidium Draba, Alyssum calycinum*, are a few examples, and the selection shows incidentally that the range of the cruciferous plants in question extends from the extreme North to the latitude of the Sahara, and from high altitudes to the level of the deep-lying steppes; in fine, that this same process of autogamy recurs under the most diverse external conditions. All these Cruciferæ are protogynous, and have six stiff stamens, four long and two short. The anthers of the former are still closed when the flower opens, but are already on the same level as the stigma. Autogamy is, however, prevented immediately on the dehiscence of the anthers, owing to there being a little horizontal interval between them and the stigma. It is not till the flower is almost over that the erect filaments move sufficiently towards the middle of the flower to deposit the pollen upon the stigma. The pollen of the shorter stamens does not get transferred at all to the stigma in the same flower except in a few species. It is carried away by insects and used for cross-fertilization, whilst the pollen of the longer stamens mainly subserves the purpose of autogamy. *Lepidium Draba* exhibits a curious contrivance to prevent the four longer stamens from being touched by insects and despoiled of their pollen during the first part of the time that the flower is open. The stamens referred to bend outwards and hide themselves for a time behind the petals. The advantage of this movement is that in no circumstances can there be a deficiency of pollen for the ultimate process of autogamy. In *Hutchinsia alpina* usually only one of the four longer stamens approaches sufficiently near to the stigma to cover it with pollen, and after it has effected this object, it removes itself again away from the axial position. All these movements are performed as a general rule with great rapidity. In *Alyssum calycinum* they take a few hours, in *Draba verna* the interval between morning and evening.

Some annual species of the Wood-sorrel genus—such as *Oxalis stricta*, for example—have five short and five long stamens in each flower. The anthers of the latter are of the same height as the stigmas, but begin by being at a little distance from them, so that at this period cross-fertilization may be effected by insects alighting upon the stigmas. Within the space of a few hours, however, the longer stamens incline towards the stigmas and deposit their pollen upon them. Here, again, the pollen of the five shorter stamens does not reach the stigma in the same flower, but is devoted to cross-fertilization. As in these annual species of Wood-sorrel, so also in the majority of species of St. John's-wort (*Hypericum*), the unequal length of the stamens, combined with the fact of the non-simultaneity of sexual maturity (*dichogamy*), is of advantage to the plant in that it ensures that autogamy shall take place just before the flower fades, whilst permitting at an earlier period cross-fertilization by the pollen of other flowers through the agency of insects. In *Hypericum perforatum*, which may be chosen as our example, the pistil is encompassed by a number of filiform filaments of unequal lengths, so arranged that the longest are in close proximity to the central pistil and the shortest near the periphery of the flower. The anthers do not liberate their pollen simultaneously, but one group does so after another. Dehiscence takes place first in the short stamens, next in those of median size, and last of all in the long ones. As soon as an anther opens, the filament bearing it inclines inwards, and thus one after another, the short, median, and long filaments stand up and approach the middle of the flower. It being only the anthers of the longest stamens that are on the same level as the stigmas, autogamy cannot occur till quite at the last, not long before the flower withers.

The widely-distributed Star of Bethlehem (*Ornithogalum umbellatum*) exhibits on the opening of the flower six stamens arranged in two whorls with three in each whorl. The stamens of the inner whorl are the longer, and their anthers dehisce a day sooner than the others. All six filaments look erect in the newly-opened flower, but are really sloped slightly outwards, with the result that the anthers are separated by an interval of about 3 mm. from the small stigma in the middle of the flower. So long as they maintain this position the pollen cannot be directly deposited upon the stigma, and the aim of the flower at this stage is to secure cross-fertilization through the intervention of honey-seeking insects. Towards the end of the flower's period of bloom both the long and the short stamens approach the centre, but only the anthers of the three shorter ones are applied to the stigma and besmear it with pollen; the other three do not come into contact with the stigma owing to their standing at a higher level. Thus the Star of Bethlehem differs from the cases previously described in that it devotes the pollen of the shorter stamens to autogamy and those of the longer stamens to heterogamy (cross-pollination). This is partly due to the circumstance that the anthers of the three longer stamens are placed just in front of the approach to the nectaries of the ovary and in such a position are certain to be brushed by insects, whilst no honey is to be found behind the anthers of the three shorter stamens, and insects, therefore, make no attempt to enter past them. These anthers, consequently, retain their pollen, and when the flower is nearly over yield it up for the purpose of autogamy.

A curious contrivance is exhibited by *Aphyllanthes Monspeliensis*, a plant indigenous to Southern Europe. Like the Star of Bethlehem, it has three long and three short erect stamens in each flower, and the anthers are not at first in contact with the stigma. But before the final closing of the perianth all the stamens slope towards the stigma, which is subdivided into six lobes, three at the top and three lower down, so that the pollen of the three shorter stamens is deposited on the lower stigmatic lobes, and soon afterwards that of the three longer stamens is deposited on the three upper stigmatic lobes.

In many plants where all the stamens are of the same length, and where the anthers are already on the same level as the stigma at the time when the flower opens, the process of autogamy is essentially identical with that above described. The anthers are held by erect filaments at a little distance from the stigma, but later on, after various movements have been accomplished by the filaments, they adhere to the stigma and deposit their pollen upon it. This is the case, for instance, in *Paris quadrifolia*, in several species of *Scilla*, in *Chelidonium* and *Rœmeria*, in *Samolus Valerandi*, in *Androsace elongata*, *A. maxima* and *A. septentrionalis*, in *Lysimachia nemorum* and in *Swertia perennis* and *S. punctata*. It is not possible here to discuss all these plants individually, and only a few points in connection with them will be referred to. In the Herb Paris (*Paris quadrifolia*) the period during which each flower remains open is very long. The stiff stamens at first stand out radially, but later they describe an angle of 80° towards the middle of the flower, where they converge over the pistil and press their anthers upon the stigmas. In the plants of the order Primulaceæ—viz. *Samolus Valerandi*, *Androsace elongata*, *A. maxima*, and *A. septentrionalis*—the corolla is salver-shaped, and the short filaments, which are adnate to the tube of the corolla, only need to incline slightly towards the axis in order to transfer their pollen to the stigma in the same flower. The majority of these plants are protogynous; the flowers of *Swertia perennis* and *S. punctata* alone are markedly protandrous. There is, therefore, in the case of the latter no chance of cross-fertilization at the beginning of the period of flowering, the stigma being still closed. On the other hand, pollen is available for transport by insects to flowers that happen to be at a later stage of development. The next step is for the stigma to open and so dispose its two lobes that flies arriving with a supply of pollen from younger blossoms are obliged to effect cross-fertilization. To prevent restriction or frustration of this process of heterogamy, and also to ensure the preservation of some pollen for autogamy in the opposite case of an absence of insect-visitors, the five stamens bend outwards simultaneously with the opening of the stigma, exserting their anthers and hiding them under the stellately-expanded petals. If no insects come, and cross-fertilization is therefore excluded, the filaments straighten themselves again and then move like the hands of a clock towards the middle of the flower, where they press their anthers, which still retain a little pollen, upon the stigma.

The stamens, which are instrumental in effecting autogamy by movements of inclination in the direction of the stigma, are straight at the commencement of the period of flowering in all the plants above enumerated. Sometimes they curve outwards for a short time, but before the flower fades, and particularly at the moment of autogamy, they are invariably erect again.

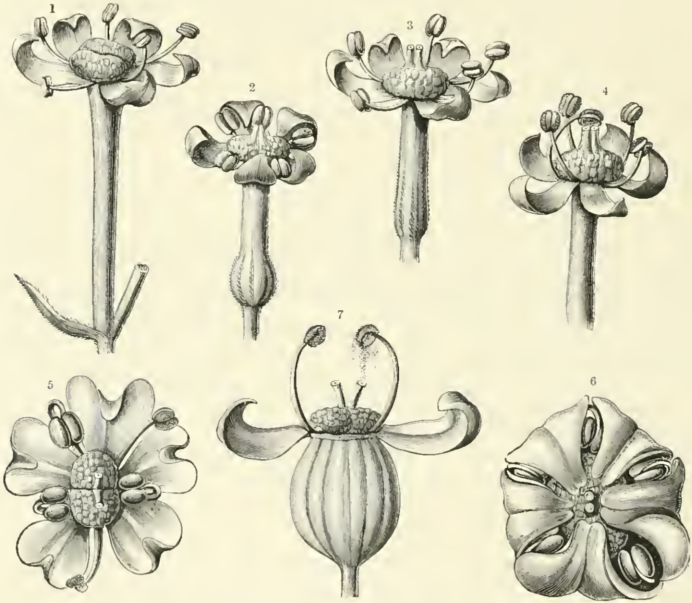


Fig. 296.—Autogamy effected by the inclination of curved stamens.

^{1} Pseudo-hermaphrodite male flowers of the Venus' Comb (*Scandix Pecten-Veneris*). $^{2, 3, 4}$ Successive positions assumed by the true hermaphrodite flowers of the Venus' Comb at first with a view to cross-fertilization, afterwards with a view to autogamy. $^{5, 6, 7}$ Successive positions assumed by the true hermaphrodite flowers of the Fool's Parsley (*Æthusa Cynapium*) at first with a view to cross-fertilization, afterwards with a view to autogamy. All the figures magnified.

There is, however, another group of plants to be considered in which the filaments are already inflexed in the bud, and continue so at the time when pollen from the anthers at their extremities is deposited upon the adjacent stigmas. The most important examples of plants exhibiting this autogamy by means of an inclination of inflexed filaments are afforded by several annual Umbellifers with protogynous flowers (*Æthusa Cynapium, Caucalis daucoides, Scandix Pecten-Veneris, Turgenia latifolia*, &c.). Two kinds of flowers are associated together in the umbels of the Venus' Comb (*Scandix Pecten-Veneris*; see fig. 296 $^{1, 2, 3, 4}$), namely, pseudo-hermaphrodite (*cf.* p. 294) male flowers (fig. 296^{1}) and true hermaphrodite flowers (figs. 296$^{2, 3, 4}$). The latter open earlier than the former, which, indeed, never come into play until the hermaphrodite flowers have cast both stamens and petals. Directly the petals open in the hermaphrodite flowers a finely-granulated honey-secreting disc and two short styles are revealed in the middle of the flower. The stigmas at the extremities of the styles are already mature, but the stamens are incurved like hooks and have their anthers still closed (fig. 296^{2}). The day after, also, when the petals have opened further back and the filaments have straightened out (fig. 296^{3}), the anthers surrounding the stigma in a circle are still closed, so that pollination can only take place at this period in the event of insects bringing pollen from other flowers. The anthers and filaments have, however, now entered upon an active phase. The curved stamens bend successively at short intervals, one after the other (after one has started, the next to follow is the stamen next but one to the left, and so on till all have done) towards the centre of the flower, bringing their anthers, which have meanwhile undergone dehiscence and are covered with pollen, into contact with the stigmas precisely in the manner shown in fig. 296^{4}. Each stamen only stays a short time in this position, and then executes a backward movement and makes way for the next in order. When all the stamens have accomplished these evolutions, they as well as the petals become detached and fall to the ground. The secretion of honey

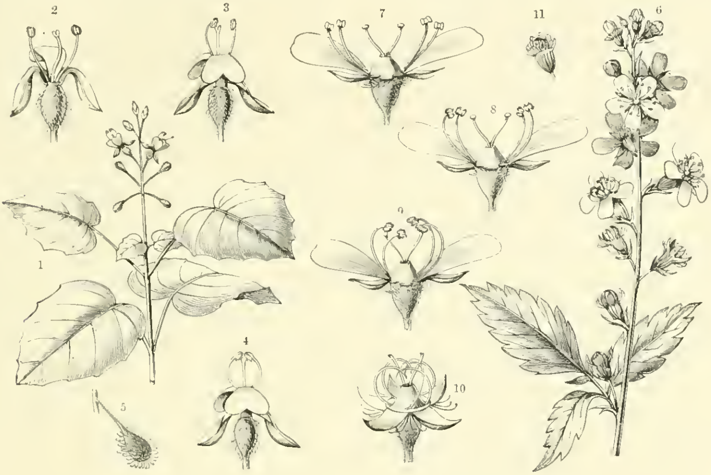


Fig. 297.—Autogamy effected by inclination of curved stamens.

^{1} *Circæa alpina.* ^{2} A newly-opened flower of *Circæa alpina* with the front petal removed. $^{3, 4}$ The same flower at a later stage of development. ^{5} Fruit of *Circæa alpina.* ^{6} *Agrimonia Eupatoria.* $^{7, 8, 9, 10}$ Successive phases of a flower of *Agrimonia Eupatoria*, which is at first adapted to heterogamy (cross-pollination) and subsequently to autogamy. ^{11} Young fruit of *Agrimonia Eupatoria.* $^{1, 6, 11}$ natural size; the rest of the figures magnified.

on the rough surface of the pad of tissue in the middle of the flower ceases, the pollinated stigmas turn brown, and the period of bloom for that particular flower comes to an end. The imperfect staminiferous flowers do not unfold until all the hermaphrodite flowers are over, a fact which can only be interpreted as indicating that their pollen is to be devoted to the fertilization of protogynous hermaphrodite flowers of other individuals which are still in the first stage of flowering. Fool's Parsley (*Æthusa Cynapium*, see figs. 296 5, 6, 7) differs from the Venus' Comb and the other annual Umbellifers above referred to in that all the flowers of an umbel are hermaphrodite, and that the filaments, which in the bud are tucked in like springs (fig. 296 5), not only straighten out when the flower opens, but elongate, and thus raise the anthers to a higher level than the stigma. Also in Fool's Parsley, as has been mentioned before, the anthers are not laid right against the stigmas, but remain a little higher, and let their pollen fall upon them from above (see fig. 296 7). This at least is what I saw in the case of the common Fool's Parsley or *Æthusa Cynapium*; the small *Æthusa segetalis*, on the other hand, according to my observation, much more frequently brings its anthers into contact with the stigmas in the same manner as the Venus' Comb (see fig. 296 4).

Autogamy of the same type as that described in the above instances of annual Umbelliferæ also takes place in many small-flowered Bed-straws (e.g. *Galium infestum*, *G. Mollugo*, *G. tricorne*), in the Dodder (*Cuscuta*), in the Alpine Enchanter's Nightshade (*Circæa alpina*), and in Agrimony (*Agrimonia Eupatoria*). Of the Enchanter's Nightshade (see figs. 297 1, 2, 3, 4), it is only needful to note that the number of stamens is limited to two, and that sometimes one anther alone is laid upon the stigma (297 3), but not infrequently both subserve the purpose of autogamy in that manner (297 4). In the latter case the stigma looks as if it were grasped by the two limbs of a pair of tongs. The flowers of Agrimony have from 12 to 20 stamens, and are protogynous. The anther-filaments are very slightly incurved, each corresponding to about a sixth part of the circumference of a circle (fig. 297 7), but as soon as dehiscence takes place the filaments bend one after another towards the centre of the flower (see fig. 297 8) until they are in the form of semicircles, and some of the anthers covered with pollen come into direct contact with the stigmas, which are still in a receptive condition (fig. 297 9). Soon after the stigmas have thus been furnished with pollen the anthers drop off the filaments, and the latter coil up still more as is shown in fig. 297 10.

Several species of Stonecrop (e.g. *Sedum annuum*, *S. atratum*, *S. dasyphyllum*), and some House-leeks (e.g. *Sempervivum montanum*, *S. Ruthenicum*) have two kinds of stamens in each flower, namely, those inserted in front of the sepals and those inserted opposite the petals. The anthers of the former are the first to open, and as they are quite close to the stigmas only a slight inclination of the curved filament is necessary to bring about autogamy. After a deposition of pollen upon the stigmas has already taken place, the filaments opposite the petals also curve over inwards, and the anthers, which meantime have undergone dehiscence, are held right over the stigmas. But, seeing that the latter are by this time withered and have no further need of pollen, we are bound to infer that this fresh supply is offered for the purpose of effecting by insects' aid the fertilization of other flowers in which there is as yet no available pollen although the stigmas are accessible and mature. Opuntias and all the numerous species of the Rose genus (*Rosa*) behave in a similar manner. In them also some of the anthers devote their pollen to autogamy, whilst the others devote theirs to cross-fertilization. The filiform filaments are curved and of unequal lengths. The anthers borne by the innermost whorl of filaments open first, but their pollen is of no use for autogamy, notwithstanding the proximity of the stigmas, because the anthers are lower than the stigmas and do not spontaneously come into contact with them. Only the filaments of the outermost whorl are of the right length, and these alone curve over and lean towards the middle of the flower until their anthers rest immediately upon the stigmas. As, however, these anthers are the last to dehisce, autogamy does not ensue till the very last moment of flowering; for the whole of the time up till now the flower is adapted to cross-fertilization only.

In a number of Ranunculaceæ, such as *Anemone Hepatica*, *A. Transsylvanica*, *Ranunculus alpestris*, *R. acer*, and *R. montanus*, the structure of the flowers resembles to a certain extent that of Roses. A group of pistils with short styles and almost sessile stigmas rises up in the middle of the flower, and is surrounded by a large number of stamens which are arranged in several whorls and are in their turn encompassed by the petaloid sepals. The flowers are protogynous, and at the commencement of their period of bloom can only undergo cross-fertilization through the agency of insects. At a subsequent stage also after the dehiscence of the anthers of the outer whorl and the exposure of their adhesive pollen, the flowers are still adapted to heterogamy; for the distance of these anthers from the stigmas is comparatively great, and insects always alight on the group of carpels in the centre and make their way from them over the anthers to the circumference, whence they again take flight in order to visit another flower. But by degrees the stamens of the inner whorl also mature; the filaments, which hitherto have been very short, grow considerably and curve inwards, laying upon the stigmas their anthers which have meanwhile burst open. The sepals of these Ranunculaceæ close up when it begins to get dark, and the flowers assume a nodding position owing to a slight inflection of their pedicels. It might be supposed that these movements also are accessory to autogamy, and, as a matter of fact, in many other Ranunculaceæ, which will be the subject of discussion later on, such co-operation does occur; but, in the Anemones and Ranunculuses above referred to, no supplementary action of the kind is necessary, and the closing and nodding of the flowers in wet weather and during the night are resorted to merely with the object of protecting the pollen from moisture.

To this long list of plants with protogynous flowers must now be added a few protandrous species from the genera *Gypsophila*, *Saxifraga*, and *Cuphea*. The flower of *Gypsophila repens* contains ten stamens, of which five are inserted in front of the sepals and five in front of the petals. In the bud they are all tucked in like hooks; in the open flower they are straight and slope outwards. Contact with the central stigmas, which meanwhile have become mature, is impossible so long as the stamens maintain the latter position; but shortly before the flower fades, the stamens become inflexed, and their anthers are thus brought against the stigmas. The Saxifrages also have two circles of stamens in each flower. In the species of the sub-genus Cymbalaria (*Saxifraga Cymbalaria, S. Huetiana,* &c.), the first to straighten out are those standing opposite the sepals. Their anthers open and display their pollen at a time when the adjacent stigmas are closed together, and are not as yet capable of taking up pollen. This supply of pollen is not therefore used for autogamy, but is obviously available for crossing with other flowers. After exposing their pollen one after another in definite order for a couple of days, these stamens incline outwards and let their anthers fall. The styles, now, for the first time, move asunder, and their stigmas become capable of receiving pollen. As the anthers of the stamens opposite the sepals have dropped off, and those of the stamens opposite the petals are still closed, the stigmas are only liable at this stage in the development of the flower to be dusted with pollen from other flowers or other plants. Eventually signs of vitality are also exhibited by the stamens opposite the petals. They become strongly inflexed, their anthers dehisce, and, the stigmas being still receptive, the period of the flower's duration is brought to a close by the anthers being pressed against the stigmatic surface and effecting autogamy. The same sort of thing is observed in the case of the protandrous flowers of several species of the genus *Cuphea*, as, for instance, in *Cuphea eminens.* These flowers, of which mention has already been made on p. 235 (figured on p. 237), face sideways and contain eleven stamens of varying length whose anthers are disposed in two irregular rows above the expanded calyx-tube. The style is short at the commencement of flowering, and is concealed, together with the immature stigma, underneath the anthers. Dehiscence occurs on the upper faces of the anthers which are turned away from the style, and the pollen issuing from the sutures is fated by its position to be rubbed off by honey-sucking insects, and to be eventually used for cross-fertilization. Two days later the style, which has in the meantime increased in length some 11 mm., projects above the stamens, bringing the stigma into the line of entrance to the honey (fig. 262 ^{2}, p. 237). Should insects now visit the flower, bringing with them foreign pollen, cross-fertilization is certain to ensue. But, in the event of an absence of insects, the longest stamen bends up to the stigma and presses that face of the anther which is coated with pollen against the stigma.

The degree of inflection of the filaments in the cases hitherto described scarcely corresponds to the third of the circumference of a circle, and is but seldom actually spiral. But that more pronounced movements of inflection do occur for the purpose of effecting autogamy, is shown by the case of *Nicandra*, a plant belonging to the Solanaceæ, and that of *Calandrinia compressa*, belonging to the order Portulaceæ. In *Nicandra* the long filaments bend down to the extent of at least a semicircle to reach the stigma in the event of a failure of pollen from extraneous sources, and in the ephemeral flowers of *Calandrinia compressa*, the filiform filaments curve gently away from the velvety stigma at 9 A.M., *i.e.* shortly after the expansion of the petals, whilst three or fours hours later, when the petals close up again, they undergo spiral inflection from right to left and lay their anthers upon the stigmas.

The cases in which the stigmas are the agents in the operation of transfer to themselves of pollen from the anthers of the same flower may be classed in two divisions, (1) those in which a direct contact between the stigma and the anthers is effected by some definite bending or other movement of particular parts of the pistil; and (2) those in which the pollen is first deposited by the anthers and stored in some part of the flower other than the stigma; ultimately the stigmatic tissue is brought in contact with it in the same manner as in (1), *i.e.* by some movement on the part of the pistil.

The cases comprised in the first division fall naturally into four groups.

To the first group belong all those in which autogamy is produced by *contraction* of the style. The Cactiform plants of the Mexican plateaux, in particular, various species of the genera *Cereus, Echinopsis,* and *Mammillaria,* exhibit in their flowers a number of filiform stamens, arranged in a close spiral around the passage leading to the honey secreted on the floral receptacle. In the midst of this thicket of stamens stands a long style which terminates in a stellate stigma. The anthers are already covered with pollen when the petals unfold, but the stigma, which projects considerably beyond the anthers, is still closed, its fleshy lobes being coherent and forming a kind of club, so that there can be no possibility of its being dusted with pollen. Thus the flowers are markedly protandrous, and the pollen liberated during the first part of their period of bloom can only be used for cross-fertilization. The next step is the opening of the stigma and spreading out of its lobes into a star in front of the entrance to the nectary. Insects now alighting are obliged to brush against the stigma before they can get at the nectar, and in so doing they deposit a portion of the store of foreign pollen with which they are laden upon the stigma and initiate a process of cross-fertilization. This stage may last a few hours only, or several days, or over a week, according to the species. When the term of the flower's duration is nearly reached the style contracts in length, and the stigma, which has hitherto been above the anthers, is drawn into the midst of them, so that it cannot fail to get covered with the pollen, of which there still remains a quantity clinging to the anthers. In *Cereus dasyacanthus* the stigma soon after the opening of the flower projects 1 cm. beyond the anthers. The length of the style bearing the stigma is at that time 20 cm. When the flower is nearly over, the style is only 16·5 cm. long, and the stigma is therefore drawn in through a space of 3·5 cm. and no longer surmounts the stamens, but, on the contrary, is 2·5 cm. lower than the anthers of the longest stamens.

The second group includes all cases where autogamy is brought about by an *elongation* of the ovary or the style. *Epimedium alpinum,* a native of the warm valleys of the Southern Alps, has four sepals arranged crosswise and beneath these —the flowers being partially inverted as shown in figs. $298^{1, 2, 3}$—four petals fashioned like little slippers and containing an abundance of honey in their blunt saccate interiors. The ovary is spindle-shaped, and bears at the end of a short style a stigma covered with little papillæ. The stamens, four in number, rest with their dorsal surfaces in contact with the ovary; their anthers face outwards, are lanceolate in shape, and each carries on its apex a small foliaceous scale like the point of a spear (see fig. 298 [4]). The flowers are protogynous, or, in other words, the papillose stigma, which is hemmed in by the four scales just referred to, is already mature at a time when the anthers are still closed (fig. 298 [1]). At this stage the stigma may be dusted with pollen from other flowers. The next step is the dehiscence of the bilocular anthers, which takes place in a very peculiar manner. The wall of each anther-half which faces outwards becomes detached, and is lifted up in the form of a flap with the whole of the pollen of the corresponding cavity sticking to its inner surface. The two flaps then shrivel and roll up, with the originally internal surface outside, until the only point of attachment is just below the pointed scale at the apex of the anther; the free flaps arch over this foliaceous anther tip (fig. 298 [5]), and also over the stigma, which is close to the scale (fig. 298 [2]). The process is simultaneous in all four anthers, the result being that the stigma is roofed over by a vault composed of eight curved flaps, and as the exposed surfaces of the latter are thickly coated with pollen, the whole arch presents externally a continuous covering of that material (see fig. 298 [2]). Should insects now visit the flower to obtain the honey stored in the slipper-shaped petals they must brush past this pollen-covered vault; nor can they fail to be besmeared at the very spot where at a previous stage in the flower's development they would have had to brush against the stigma. This condition of affairs lasts usually for two days. In the meantime changes affecting the pistil are taking place which, notwithstanding their inconspicuous nature, are of the greatest importance in relation to the eventual accomplishment of autogamy. If the stigma is not dusted by insects with foreign pollen at the first expansion of the flower the pistil now elongates sufficiently to raise the stigma into the vaulted cavity just described; and as the flaps composing the vault curl up still more (fig. 298 [6]) as the flower approaches its end, the stigma must inevitably come into contact with the pollen adherent to them (cf. fig. 298 [3]).

A similar process is observed to take place in several Cruciferæ, of which the Charlock (*Sinapsis arvensis*) is a typical instance. The flowers of this plant are protogynous. The bud opens early in the morning, revealing still closed anthers with their faces turned inwards (*introrse*), whilst the stigma is already mature and projecting somewhat above the anthers. At this stage of development no pollen except what is brought by insects can be deposited on the stigma. A day later the flower presents quite a different appearance. The four longer stamens have stretched and curved a little away from the axis, and the anthers are lifted above the stigma. By a rapidly executed twisting of the filaments the anthers have been turned round so as to face outwards, and extrorse sutural dehiscence has meantime taken place. The stigma is completely withdrawn from observation, and is also safe from any possibility of being dusted with pollen, for the anthers in the same flower have turned away their pollen-coated faces, nor is it possible for any extraneous pollen that may happen to be brought by insects to be transferred to the stigma, owing to the anthers forming a hood over it. At this stage every other object is subordinated to the dispersion, through the agency of insects, of the pollen exposed by the flower. After the interval of another day the observer finds a third aspect of the flower presented to him. The filaments have straightened themselves out, and so brought the anthers nearer to the stigma; the coating of pollen has spread all over the anthers, and the ovary has undergone elongation, carrying the stigma into the midst of the dome of anthers, where it becomes thickly overlaid with pollen

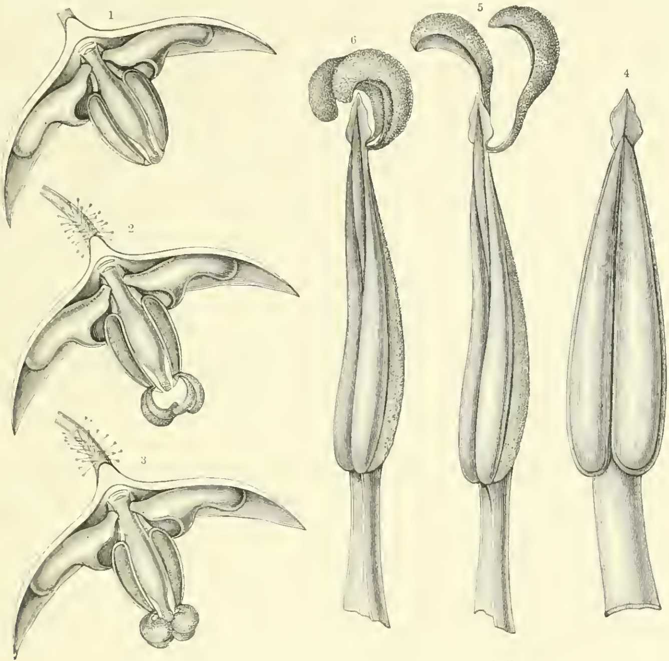


Fig. 298.—Autogamy brought about by elongation of the pistil.

$^{1,\,2,\,3}$ Flower of *Epimedium alpinum* at successive stages of development, showing primary adaptation to cross-fertilization and subsequent adaptation to self-fertilization. ^{4} Front view of a closed anther. ^{5} Side view of the same The front (right-hand) wall of each of the two loculi has become detached and been raised up as a flap or valve. ^{6} The same anther; the flap has curled up more tightly and now forms a sort of cowl arching over the spear-like apex. $^{1,\,2,\,3} \times 10$; $^{4,\,5,\,6} \times 25$.

Again, in the nodding flowers of *Atragene alpina*, and in these of *Clematis integrifolia*, which grows freely in the swampy meadows of the Hungarian plains, we find autogamy effected by means of an advance of the pistil into proximity to the anthers laden with pollen. Both plants are protogynous—the stigmas being mature for a short time before the anthers dehisce—and in both the newly-opened flowers are adapted to cross-fertilization. The stamens lie one upon another like the tiles of a roof, and together form a short tube at the bottom of which are a number of closely-clustered carpels, whilst at the free edge of the tube the anthers expose their store of pollen. The first anthers to open are those pertaining to the outermost and longest stamens, the next belong to those of median length, and the last to the shortest, which are in the immediate vicinity of the carpels. The pollen of the outermost anthers serves mainly for cross-fertilization, and can hardly ever be used for autogamy on account of its position; but even in the case of the latest anthers belonging to the shortest stamens, no pollen could reach the stigmas were it not for the elongation of the carpels, which occurs during the last two days of the flower's duration. The anthers still contain pollen at this late period, and a quantity adheres, besides, to the silky hairs clothing their filaments, so that the slightly divergent stigmas get covered with an abundant supply of pollen as the carpels lengthen and push them up through the pollen-coated tube (see fig. 246 ^{3}, p. 174).

The flowers of the Lady's Mantle (*Alchemilla vulgaris*) are likewise protogynous. When a flower opens, the anthers of the four short stamens are still closed, whilst the stigma is already mature, and is seen in the middle of the flower projecting through and slightly above a kind of diaphragm which is stretched across the floral interior and secretes honey. At this stage cross-fertilization alone is possible; but in the course of twenty-four hours the style grows in an oblique direction, until its extremity bearing the stigma strikes against one of the four anthers, which have meanwhile undergone transverse dehiscence; it thus receives a sprinkling of pollen (see fig. 226 ^{5}, p. 125). The pollen of the three other anthers is still available for transference by flies to the stigmas of other flowers.

The above are a few instances of the methods in which autogamy is effected by elongation of the style or of the entire pistil. Taken generally this process must be classed among the rarer forms of the phenomenon, though it is surprising that it should be so considering the frequency of autogamy by means of the elongation of stamens. The accomplishment of autogamy through the *inclination* of a style otherwise straight is of even less usual occurrence. The most striking example of this process is afforded by the bilabiate flowers of the North American *Collinsonia Canadensis*. In the newly-opened blossom the long style stands midway between two exserted stamens which are almost as long as the style. Towards the end of the flower's period of blossom, the style begins to slope towards one of the stamens, moving like the hand of a clock through an angle of from 20° to 40° until its stigma comes against the pollen-covered anther borne by the stamen in question.

A much more common method of bringing about autogamy is for parts of the pistil—usually the style—to bend so as either to bring the stigmas into direct contact with the anthers belonging to the same flower, or to place them in such a position beneath the anthers as to ensure their catching any pollen that may fall out of the loculi. The direction of the style's inflection depends upon the form and mode of insertion of the flower, and more particularly on the position assumed by the anthers. The flowers of the Great Mullein (*Verbascum Thapsus*), of the Cornsalad (*Valerianella Auricula*, *V. carinata*, &c.), and of the non-twining species of Honeysuckle (*Lonicera alpigena*, *L. nigra*, *L. Xylosteum*) are protogynous, and the style is so placed when the corolla opens that its stigma must of necessity be brushed by insects as they make their way to the receptacle. There is evidently at this stage no possibility of any but cross-fertilization. Later on, when the anthers open and expose their pollen, the stigma is taken quite out of the way, the style becoming bent downwards or to one side, so that the stigma cannot come into contact with anthers of the same flowers either spontaneously or through the agency of insects. Not till the flowering period is nearly over does the style return to its original position; when this happens, the stigma is raised by the straightening up of the style, and is pressed against the anthers, which are still coated with pollen. The flowers of the Martagon Lily (*Lilium Martagon*) are nodding, and have their perianth-lobes strongly reflexed. In each petal there is a groove which is roofed over and closed in the middle by two coalescing rims, so that the honey stored in the groove can only be sucked out by insects at the two extremities where the groove is open. The flowers are protogynous, and, when they are newly open, the style is straight and holds its stigma in such a position that it is sure to be touched by insects sucking honey from the inner orifice of the groove. As the anthers are still closed at this stage, only foreign pollen can be affixed to the stigma. Subsequently dehiscence ensues, and the position of the anthers in front of the external orifice of the groove ensures their pollen being brushed off by insects trying to suck the honey at that end, whilst the stigma is left untouched by them. In this second stage of the flower's development the style begins to bend a little to one side, and, towards the end, the curvature increases to such an extent that the stigma comes into contact with one or sometimes two of the anthers, and dusts itself with pollen. Often enough, it is true, the stigma misses its mark, and in consequence autogamy is not so certain to occur in the Martagon Lily as in most of the other cases. It

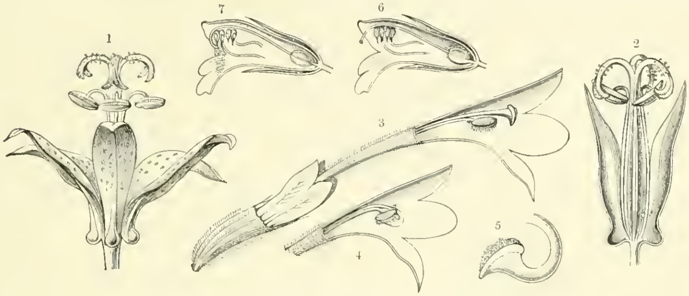


Fig 299.—Autogamy effected by means of an inflection of the style.

[1] Flower of *Tricyrtes pilosa* in the first stage of its development. [2] The same in the last stage of development. [3] Flower of *Morina Persica* in the first stage of development. [4] The same in the last stage of development [5] Stigma of *Morina* covered with pollen from anthers belonging to the same flower. [6] Flower of *Euphrasia minima* in the first stage of development. [7] The same in the last stage of development. All the figures slightly magnified. In figs [2], [3], [4], [6] and [7] the front part of the flower is cut away

must also be noted that the inflection of the style only takes place should the stigma have not previously been supplied with extraneous pollen. If there has been cross-pollination at the commencement of flowering the inflection either does not occur at all or is so trifling as to be of no significance.

The transference of pollen to the stigma by means of a bending down of the style is observed in various species of *Tricyrtes, Morina, Œnothera,* and *Epilobium,* in several Rhinanthaceæ, Caryophyllaceæ, and Ranunculaceæ, and in most of the Malvaceæ. The flowers of *Tricyrtes pilosa,* of which figures are given above, are protogynous. Each of the three styles is bent down, and has a bifurcated extremity, so that it looks not unlike a claw. The stigmatic tissue is situated at the end of the claw, and is brushed by insects on their alighting to suck honey from the saccate bases of the perianth-segments. The free extremities of the filaments curve down in semicircles, and the anthers are suspended under the claws of the style (fig. 299 [1]). At the time when the anthers have their pollen exposed they are so situated as to stand in the way of insects coming in quest of honey. Without the assistance of insects there could be no transference of pollen to the stigma so long as stigmas and anthers remained in the same relative positions, and the flower remained upright. But the chance of insects not visiting the flower is provided for by a downward bending of the claws of the style, which continues until the stigmatic tissue at their extremities comes into direct contact with the pollen-coated anthers (see fig. 299 [2]).

The process above described takes place in the course of a week in *Tricyrtes pilosa,* but in *Morina Persica,* one of the Dipsaceæ (see figs. 299 [3, 4, 5]), it is all accomplished within a few hours. The difference between the times at which stigmas and anthers respectively attain maturity in *Morina* is scarcely half an hour, but even this short interval suffices to render cross-fertilization possible during the first stage of flowering, whilst in the second stage autogamy obtains. All the species of the genus *Morina*—including *Morina Persica,* the type here selected for illustration—unfold their flowers at dusk. As soon as the corolla-limb expands the thick pulvinate stigma becomes visible in the middle of the flower just above the entrance to the honey. The receptive tissue is on the upper surface of the stigma. The two anthers are stationed behind the stigma, and when insects insert their probosces into the long honey-filled tube of the corolla they are certain to effect cross-fertilization, provided they have previously visited flowers at a somewhat later stage of development. In the case of other plants whose flowers open in the morning it would be scarcely likely that insects should alight immediately after the opening of the passage to the honey, but the flowers of *Morina* are adapted to crepuscular and nocturnal moths, which only have two or three hours of darkness in which to get the honey, and must, therefore, make great haste and employ the whole of the time if they are not to fail in their quest. As a matter of fact the moths in question leave their haunts within a quarter of an hour of the time when the flowers of *Morina* open, and one may be sure that wherever Sphingidæ and Noctuæ with probosces 3 or 4 centimetres in length abound, one or more will come flying to suck the honey as soon as the floral receptacle becomes accessible. Thus, dichogamy, involving hardly half-an-hour's interval between the attainment of maturity in stigmas and anthers respectively, is sufficient to ensure cross-fertilization at the commencement of the period of bloom in each flower of this kind of night-flowering plant. A further adaptation with a view to heterogamy is shown in the position of the stigma in front of the anther in the first stage of floral development (see fig. 299 [3]). On the intrusion of insects—Sphingidæ, Noctuæ, &c.—into the interior of the flower the large stigma is the first object encountered, and next to it come the anthers, and there is therefore a possibility that even during the time that the anthers are open and have their pollen exposed cross-fertilization may take place through the agency of insects. If, however, no insects visit the flower the style bends down the very next morning in an open curve and lays the stigma flat upon the anthers (see fig. 299 [4]). The pollen readily adheres to the surface of the stigma, as may be seen by removing that organ after it has become appressed to the anthers, when a thick layer of pollen will be found sticking to it (fig. 299 [5]).

Inflections of the style in all respects similar to those exhibited in *Morina* occur in the flowers of numerous Rhinanthaceæ, *e.g.* in *Rhinanthus minor, Trixago apula, Melampyrum pratense, Euphrasia minima* (see figs. 299 [6] and 299 [7]). In these plants we find, in general, a repetition of the entire process above described, except for the circumstance that the pollen is not adhesive but mealy, and is not transferred to the receptive tissue by appression of the stigma to the anthers—it being sufficient to place the stigma under the anthers by means of an inflection of the style. The stamens in this case are of the sugar-tongs type (*cf.* p. 271). In the first and second stages of floral development the mealy pollen only falls out of the anthers on the occasions when the stiff filaments of the stamens are forced apart by insects. Should no insects visit the flower the pollen remains in the loculi. In the third stage of flowering the filaments become flaccid, as does also the portion of the corolla adjacent to them, and in consequence the anthers, which have hitherto been closely coherent, move a little apart from one another and let the pollen fall out. Meanwhile the style has bent down sufficiently to bring the viscid stigma under the front pair of anthers, so that a portion of the pollen is caught upon its glistening surface, with the result that autogamy is effected (see fig. 299 [7]). It is not uncommon for the inflection of the upper third of the style to be so strong as to amount to an involution, and the stigma is then pushed between the disuniting anthers and comes into contact with the hairs which clothe the anthers, and which are usually powdered all over with pollen.

Tricyrtes, Morina, and the Rhinanthaceæ just mentioned, are all protogynous, whilst on the other hand, the Evening-primrose, Willow-herb, Campion, and Mallow, in which autogamy likewise occurs in consequence of the style bending down to the anthers, are protandrous. When the petals of the Evening-primrose (*Œnothera biennis, Œ. muricata*, &c.), or of the large-flowered species of Willow-herb (*Epilobium hirsutum, E. angustifolium*, see fig. 300) expand, the four branches of the style, which bear the receptive tissue and constitute the stigmas, are closely coherent, whilst a further condition, which would also render pollination impossible consists in a lateral inclination or sharp inflection of the style which removes the stigma out of the way leading to the honey. The eight anthers then stand in front of the spots where honey is to be obtained, and liberate their pollen in turn. A little later—half an hour in Evening-primroses, and 24 hours in the large-flowered species of Willow-herb—the style straightens itself and takes up a central position in the flower, whilst its four branches open back and present themselves in the form of a cross in front of the entrance to the honey. The stigmas remain in this position for a short time, and there is no need to enter into more detail to make it evident that cross-pollination may now be effected by the humble-bees which come in search of honey and bring with them a store of pollen from younger flowers. Soon afterwards, the four stigmas bend or roll back, bringing their receptive tissue into contact with the pollen still adhering to the anthers (see fig. 300, the lower flowers). This act of autogamy is usually promoted also by the stamens becoming rather more erect and by an inflection of the stalk-like inferior ovary in a gentle curve towards the ground, the result of which is that the flowers nod, *i.e.* are half-inverted.

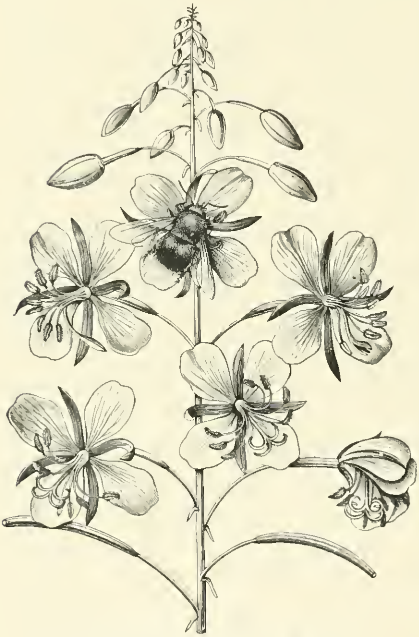


Fig. 300.—Autogamy in the flowers of the Willow-herb (*Epilobium angustifolium*).

Of the Ranunculaceæ, a few species of Love-in-a-mist (*Nigella*) exhibit the same kind of contrivance. The flowers are protandrous. The first event to take place after the expansion of the sepals is a bending of the stamens in regular sequence towards the periphery of the flower, whereby the open anthers are posted just above the nectaries full of honey. Insects coming in search of honey must inevitably rub against the anthers in that position and dust themselves with the pollen. After the stamens have all accomplished these movements, the styles, which have hitherto stood stiffly erect and stationary, enter upon an active phase and bend outwards until their terminally-placed stigmatic tissue, which, meantime, has become mature, rests over the nectaries. In this position the stigmas are certain to be dusted with pollen from younger flowers brought by the insects which come in search of honey. The process of outward inflection of the styles is, however, not yet completed, but continues until the stigmas strike against the anthers and take from them some of the pollen still clinging to their surfaces.

There are also some caryophyllaceous plants (*Lychnis alpina*, *Alsine Gerardi*, *Cerastium arvense*, *C. lanatum*, *Stellaria graminea*, *S. Holostea*) which exhibit, just before the flowers wither, inflections enabling the stigmas to possess themselves of the pollen of the anthers in the same flower. The flowers are incompletely protandrous. First of all, the stamens inserted opposite the sepals come to maturity while the stigmas in the same flower are still incapable of receiving pollen. The pollen offered by these stamens can therefore only be used for cross-fertilization. The next day their filaments bend as far as possible towards the periphery of the flower, and many of them lose their anthers. Meanwhile, the stamens standing opposite the petals grow longer and their anthers dehisce so that their pollen also is rendered available for transference by insects. A day later these stamens bend slightly towards the periphery of the flower, but they never lose their anthers, which continue to offer their pollen till the flower withers. On the fourth day the styles, which have hitherto stood in the middle of the flower, separate from one another, curve over backwards, and, in some species, become twisted into spirals. The stigmas are thus brought into contact with the anthers last mentioned and take up some of the pollen with which they are covered.

In the Caryophyllaceæ whose names are given above the inflections of stamens and styles take four or five days; in Mallows (*Malva borealis*, *M. rotundifolia*, &c.) the same processes are completed within 48 hours, and in *Hibiscus Trionum*, and in *Abutilon Avicennæ* within from three to eight hours. When the flower of a Mallow is just open a sheaf of filaments bearing round anthers covered with pollen may be seen enveloping and roofing over the styles. Soon after, however, the filaments of which the sheaf is composed become reflexed and a bundle of styles is then seen occupying the place previously filled by the stamens. The stigmatic tissue has matured in the meantime. The parts of the flower do not remain long in this position, which is obviously adapted to cross-fertilization by insect agency; the styles coil into the shape of an S and at the same time bend down until the fringe of papillæ constituting the stigmatic tissue comes into contact with the pollen of the anthers which have shortly before been lowered by the inflection of their filaments. In *Abutilon Avicennæ*, which grows abundantly in Hungary on the banks of the river Theiss, the sheaf of filaments does not at any time form a roof over the style, but, from the moment the petals unclose, five slender styles, terminating in spherical red stigmas with velvety surfaces, may be seen projecting above the anthers. Insects alighting upon the velvety stigmas or brushing against them may cause heterogamy at this period; but a couple of hours later the styles curve down, and the stigmas are appressed to the anthers which are covered with an abundant store of pollen. Other Malvaceæ, *e.g.* *Anoda hastata*, behave in an opposite manner as regards the inflection of the style. In the buds of these plants both filaments and styles are sharply bent over towards the floral receptacle. After the expansion of the petals, the filaments straighten out and together constitute a sheaf of filiform stalks, each of which bears an anther covered with pollen. A little later it is the turn of the styles to become erect. They perform the same movements as have previously been executed by the stamens, and push themselves into the midst of the stamens. By these evolutions the stigmas of the longer styles are placed a little above the anthers, whilst those of the shorter styles are brought into direct contact with the anthers, and take from them some of the pollen of which there is always a certain quantity left so that autogamy invariably ensues.

The method of self-fertilization adopted by the Sun-dew (*Drosera*) is somewhat like that just described. In *Drosera* the spherical ovary supports three styles, each of which divides into two spatulate lobes bearing the stigmatic tissue on their upper surfaces. The open flower is cup-shaped, and in it these lobes may be seen spread out horizontally like the spokes of a wheel (see fig. 279[10], p. 279). The stamens, on the other hand, are erect, and cross the lobes at right angles, holding the anthers above the stigmatic tissue. As soon as the petals begin to close, the stigmatic lobes rise up until they touch the anthers.

In several Labiates and Lentibulariaceæ autogamy is dependent on inflections, not of the style but of the stigma. This occurs, for instance, in the Hemp-Nettle (*Galeopsis ochroleuca, G. Tetrahit,* &c.), where the flowers are protandrous, and so adapted as to ensure cross-fertilization in the event of insects visting them. Towards the end of the flower's period of bloom the stigmatic extremity of the lower arm of the style bends downwards and backwards until it touches the pollen-coated anthers of the longer stamens; in the case of many species of the Wound-wort genus (*Stachys palustris, S. sylvatica,* &c.) both stigmatic arms bend down a short time before the flower fades and take the pollen from the anthers. The flowers of the Butterwort (*Pinguicula*; see vol. i. plate II. p. 142), which face sideways, contain two ascending stamens terminating in patelliform anthers, and above them an egg-shaped ovary surmounted by a large lobate sessile stigma. The lower border of the stigma which bears the receptive tissue hangs down like a curtain over the anthers. Insects, in the act of inserting their probosces into the honey-containing spur, brush first against this stigmatic border, and next against the anthers behind it. Thus they dust the stigma with the pollen they bring from other flowers, and the next moment load themselves with a fresh store which they carry off to yet other plants. The conditions are, in the first instance, adapted to cross-fertilization, and very frequently this form of reproduction occurs in the plants in question; but if no insects visit a flower the pendent stigmatic border rolls up sufficiently to bring the receptive tissue against the anthers. There being still plenty of pollen on the anthers, autogamy is then certain to ensue. The same phenomena may be observed in flowers of the Bladder-wort (*Utricularia*), and probably in those of the majority of Lentibulariaceæ.

A comparatively rare method of autogamy is for both filaments and style to coil up in spirals and become entangled just before the flower fades, the stigmas being brought in the process of involution into contact with the pollen of one or more anthers. Most of the plants which exhibit this curious phenomenon have the common property of being ephemeral, but they belong to most different families. In a number of Commelynaceæ—*Commelyna cœlestis*, for example (see fig. 301)—the stigma is situated in front of and lower than the anthers when the flower, which faces sideways, is quite newly open (fig. 301[1]). Honey is secreted on curious palmately-lobed nectaries, and if in this first period of the flower's development insects come in quest of the honey they make use of the anthers to alight on, and in so doing besmear themselves with the pollen, which is already emerging through the lateral sutures of dehiscence of the anthers. Soon afterwards the stamens become spirally coiled, and the style, which meanwhile has grown to the same length as the stamens, curves in such a manner as to bring the stigma to a somewhat higher position than it previously occupied, and to make it the most convenient place for insects to settle upon (fig. 301[2]). The arrival of insects which have visited younger flowers is at this stage sure to be accompanied by cross-fertilization. This state of affairs, however, only lasts a very short time. The style then winds itself into a spiral, and becomes entangled with the coiled stamens, with the inevitable result that the stigma comes into contact with one or other of the anthers, and gets covered with pollen (fig. 301[3]). The whole process occurs in almost exactly the same manner in the flowers of *Allionia violacea*, of *Mirabilis Jalapa*, and several other Nyctaginaceæ. As regards *Allionia violacea*, it is only necessary to observe that the flowers are protogynous, that the stigma is higher than the anthers at 6 a.m., when the flower opens, that a few hours later the anthers are raised to a higher level than the stigma in consequence of certain peculiar movements of the style and stamens, and that by 10 o'clock the involution of the filaments resulting in autogamy has already begun. In the newly-opened flower of the Marvel of Peru (*Mirabilis Jalapa*) the dot-like stigma is situated in front of the anthers, and in the event of insects coming in search of honey, it is first the papillæ of the stigma and afterwards the anthers that are touched by the intruders. No raising and lowering of filaments or style takes place in this case,

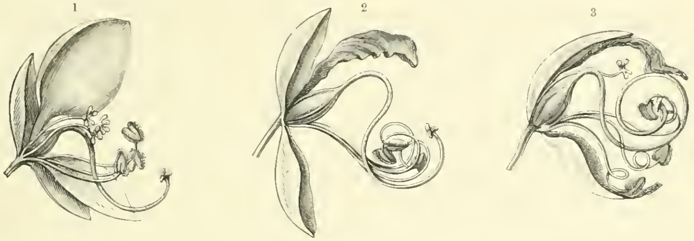


Fig. 301.—Autogamy by means of spiral twistings of stamens and style.

[1] Flower of *Commelyna cœlestis* in its first stage. [2] In its second stage. [3] In its third stage of development. All in longitudinal section and slightly magnified.

but a process of involution like that exhibited in *Allionia* ensues, and as soon as autogamy has been initiated the limb of the perianth folds up, turns pulpy, and then forms a kind of stopper above the knot of twisted filaments and style. The flowers of the Purslane (*Portulaca oleracea*) differ from those of *Commelyna, Allionia,* and *Mirabilis* in having five stigmas which are like delicate feathers in form, and are spread out in a star in the middle of the erect flower-cup. The stamens project obliquely from the receptacle, and are arranged in a circle round the stigma; but when the flower opens first, there are little spaces between anthers and stigmas, and this prevents a spontaneous transference of pollen to the stigmas. After the lapse of a few hours the petals, which in the sunshine are expanded in the form of a cup, draw together, and the flower begins to close up; all the five feathery stigmas bend over to the same side and gradually coil up into spirals. The thread-like stamens also undergo inflection, at first into semicircles, and subsequently into spirals, and the pollen-coated anthers are in consequence pressed against the stigmas. At this period, in the Purslane as in the Marvel of Peru and other plants whose flowers are ephemeral, the petals may be seen in a pulpy condition covering over the knot of tangled filaments.

As has been said before, this form of autogamy occurs chiefly in flowers which last only a single day. Where the whole period during which the flower is open is but a few hours the movements in question may all be followed by the observer. In the few species, which resemble the foregoing in respect of autogamy, but differ from them in that their flowers remain open two or three days, or even longer, these movements of inflection and torsion take place much more slowly. Thrifts (*Armeria alpina, A. vulgaris,* &c.) display in the middle of each of their cup-shaped flowers five stigmas disposed in the same manner as those of Purslane-flowers. The stigmas in this case, however, are not feathery, but in the form of slender cylinders covered with short, closely-packed papillæ, which give them a velvety appearance. The stamens are adnate to the short corolla-tube, and rise up in front of the petals holding their anthers between the rays of the stigma. Notwithstanding the proximity of the anthers to the stigmas, neither in the first nor in the second stage of the flower's development is any pollen transferred, without extraneous aid, to the receptive stigmatic tissue. At first the stamens are so placed as to have their anthers brushed by insects visiting the flower, whilst the five stigmas are still erect. A little later the anthers and stigmas change places as in so many other cases; the stamens stand up and bring the anthers together nearer the middle of the flower, whilst the stigmas diverge from one another, and place themselves close to the way leading to the honey. Attention has been so often directed to the connection between an interchange of position of this kind and the accomplishment of cross-fertilization that it is needless to repeat the facts of the case. Supposing, however, that insects do not visit the flower, and that, in consequence, heterogamy fails, the styles wind themselves up spirally, and move at the same time towards the middle of the flower, where they become entangled with the filaments, which have likewise undergone spiral torsion. In these circumstances, the velvety stigmas cannot fail to receive the pollen that still adheres to the anthers.

It appears from what has been said concerning autogamy that in a large number of plants the pollen developed in the anthers, especially if it be of the adhesive variety, still occupies the recesses of the anthers, or sticks to the reflexed margins of the lobes after their dehiscence, at the time when the flower fades. Even after insects have brushed off a portion of the pollen and transported it to other flowers, there is still invariably an abundant supply for the purpose of autogamy, and it is only in rare cases that loculi, in which adhesive pollen has been matured, are completely emptied by the end of the flowering period. In some plants, however, the adhesive pollen is swept out or removed in some other way from the anthers by means of special contrivances as soon as it is mature, and is then deposited on some particular spot in the flower where it is exposed for dispersal. In the case of the pollen of Composites it is well-known that it is pushed out of the tube of connate anthers by the style, owing to the growth of the latter organ which is sheathed within the anther-tube, and that it appears at the top of the tube in the form of a lump capping the extremity of the style. In Bell-flowers (*Campanula*), the entire contents of the anthers are stored upon the surface of the style, and the same thing happens in the various species of the Rampion genus (*Phyteuma*) and in some small-flowered Gentians. The shrivelling of the anthers is in many plants the cause of their shedding a portion of their pollen, and it may then collect on capillary appendages of the ovary, in cup-shaped petals, or on some other part of the flower where it is stored up for future use. It must often happen, too, that when insects are in the act of taking the honey they push against the stamens, and that the pollen shaken out of the anthers by their impact adheres to particular parts of the corolla, calyx, or perianth. This pollen is just as available for fertilizing purposes as that which remains sticking to the anthers, and we meet with cases where the stigmas fetch the pollen developed in the same flower from its temporary resting-place, and so bring about autogamy. Contrivances for this purpose are not numerous, but the number of species in which this form of autogamy prevails is extremely large. The abstraction of pollen deposited on the outer surface of the stylar column or its arms by stigmatic tissue situated on the edges or the inner surface of these style-branches occurs in hundreds of Campanulas and thousands of Composites, and shall therefore be chosen as our first example of this type of process.

Two modes of operation may be distinguished: first, a crossing; and, secondly, a spiral revolution of the style-branches. The former process is observed particularly in the Asteroideæ (*Aster*, *Bellidiastrum*, *Erigeron*, *Solidago*), especially in the tubular flowers in the middle of the capitula of these plants; but it is also seen in many Composites possessing ligulate flowers only. In *Aster alpinus*, the species selected for illustration (see figs. 302 [1, 2, 3]), the stylar arms are short and thickish; their inner surfaces are smooth and flat, whilst their outer surfaces are a little arched, and towards the free extremities are furnished with papilla-like sweeping-hairs. The receptive stigmatic tissue is situated on the margins of the style-branches below the sweeping-hairs, and may be recognized by the granulated appearance of its turgescent cells. The behaviour of the stylar branches from the commencement to the termination of a flower's bloom is shown in fig. 302^{1}, where the three tubular florets are in successive stages of development. Almost simultaneously with the opening of the tubular corolla the two style-branches are pushed up above the anther-tube, and the pollen is swept out of the tube by the hairs previously referred to. The style-branches at this period are in close contact, and the receptive tissue of the stigmas is not yet accessible (fig. 302^{1}, left-hand floret).

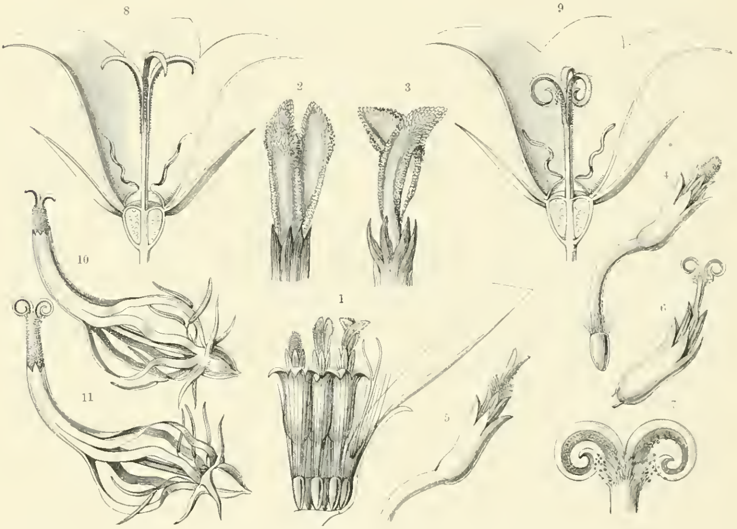


Fig. 302.—Autogamy by means of a crossing or a bending back of the style-branches.

^{1} *Aster alpinus.* Portion of a capitulum, including a marginal female floret with ligulate corolla and three tubular florets of the disc. The latter are in the successive stages which lead to autogamy (left to right). ^{2} Style-branches of *Aster alpinus* which have just separated but still have some pollen clinging to their hairs. ^{3} The style-branches crossed so as to transfer the pollen from the collecting-hairs of the one to the stigmatic tissue of the other. ^{4}, ^{5}, ^{6} Florets from the centre of a capitulum of *Centaurea montana* in successive stages leading to autogamy. ^{7} The two style-branches rolled back sufficiently to bring the stigmatic tissue into contact with the pollen on the collecting-hairs. ^{8} *Campanula persicifolia*; longitudinal section through a newly-opened flower. ^{9} The same with the style-branches rolled back so as to bring the stigmatic tissue into contact with the pollen on the exterior surface of the stylar column. ^{10} Flower of *Phyteuma orbiculare* in process of transition from the first to the second stage of development. ^{11} The same flower in the last stage of development. ^{8}, ^{9} natural size; the rest magnified.

Neither cross- nor self-fertilization of the flower in question can at present be effected, and the pollen is only exposed that it may be carried away by insects to fertilize other blossoms. The two style-branches are subsequently lifted still higher and move a little apart, with the result that the pollen clinging to their hairs, if not already removed by insects, is for the most part pushed off, falls down, and is appropriated to the purpose of geitonogamy (see p. 321). A small remnant of pollen is, however, invariably left hanging to the lower collecting-hairs, and this it is which is devoted to autogamy (see fig. 302 [2]). The process of self-pollination is the last to take place. The two style-branches bend and cross one another, and in so doing bring the pollen adhering to the lower hairs of the one arm into immediate contact with the receptive tissue on the margin of the other arm. In this position the two style-branches resemble the beak of a cross-bill, as may be seen in fig. 302 [3]. The style-branches of those Composites whose capitula consist entirely of ligulate florets, are always much longer than those of the Asteroideæ; they are of thread-like appearance, and the lower parts of their external surfaces are beset with collecting-hairs. In one section of these Composites, including, for instance, *Crepis grandiflora*, *Hieracium umbellatum*, and *Leontodon hastile*, there is likewise, shortly before the flowers fade, a simultaneous inflection and spiral involution of the two branches of the style resulting in autogamy; it reminds one, even more forcibly than the case of Asteroideæ, of the action of a person when he crosses his arms.

The second kind of process, viz. the spiral re-volution or bending back of the style-branches, may be particularly well seen in the Groundsels—*Senecio Fuchsii* and *S. nemorensis*—and in Centaureas. We will select as an example *Centaurea montana* (see figs. 302 [4, 5, 6, 7]), which grows abundantly in the lower Alps. The styles are fashioned quite differently from those of the composite flowers to which reference has been made above. The stigmatic tissue is spread out over the inner surface of the style-branches, especially over the part near the free extremity, and the collecting-hairs are confined to a narrow zone underneath the point of bifurcation of the style. The pollen is swept out of the anther-tube (see fig. 302 [4]) in the same manner as in the other Composites, but in *Centaurea* the process of extrusion is accelerated by a sudden contraction of the irritable filaments of the stamens when they are touched by insects (*cf.* p. 252). After most of the extruded pollen has been removed by insects or scattered by the divergence of the style-branches (fig. 302 [5]), the receptive inner faces of the latter are so disposed as to ensure cross-pollination in the event of insects coming laden with pollen from other capitula. This state of affairs, however, only lasts a short time; the two style-branches soon roll back and bring the receptive tissue of their originally inner faces into contact with the pollen left upon the hairs, thus effecting autogamy (see figs. 302 [6] and 302 [7]).

Bell-flowers (*Campanula*) exhibit for the most part the same bending back of the style-branches, and the phenomenon has the same significance in them as in composite flowers, but the manner in which the pollen is transferred to the external surface of the style is somewhat different. Within the closed bud the long anthers are adjacent to the central column of the style, as in Compositæ, and form a kind of tube round it. These anthers open inwards, too, and deposit the whole of their pollen on the outside of the style, which is furnished with delicate transparent papillæ, and is in consequence well adapted to the retention of the pollen. The pollen is not, however, swept out of the tube of anthers, but the anthers, after depositing their pollen upon the stylar column, separate from one another and shrivel up, and only persist as shrunk and empty relics at the bottom of the flower (see fig. 302 [8]). The style-branches are by this time divergent, and occupy a position in the mouth of the corolla, which necessitates contact between the receptive tissue at their tips and the bodies of the humble or hive bees, which find their way to the flower in search of honey. If these insect-visitors bring with them pollen from other flowers, cross-fertilization is inevitable. As they push lower down into the flower, the bees receive an additional load of pollen from the stylar column, the surface of which is coated with it, and this new store they may convey to other blossoms. When the time for the flower to fade is near at hand, the style-arms become revolute, and press the receptive tissue of their tips upon the stylar column, taking from it a coating of pollen, of which there is still a sufficient quantity clinging to the surface (see fig. 302 [9]). The large-flowered *Campanula persicifolia* has been selected as a type of these Bell-flowers. The style-arms in this species are from 1 cm. to 1·6 cm. long, and they coil into spirals of from 1½ to 2 involutions. In most of the other Bell-flowers (e.g. *C. barbata, C. carpatica, C. pyramidalis, C. Rapunculus, C. spicata*) the revolute style-branches have only from 1 to 1½ coils in each spiral, whilst in some few (e.g. *C. patula, C. rapunculoides*) there are rather more than 2 complete coils in each. The Rampion genus (*Phyteuma*), here exemplified by *Phyteuma orbiculare* (see figs. 302 [10] and 302 [11]), differs from the Bell-flowers, which are its nearest allies, in the circumstance that the deposition of pollen and retraction of the emptied anthers occurs at a time when the tips of the petals are still connate into a tube. For a short time the end of the stylar column may be seen covered with pollen projecting beyond the corolla, and in this position the two arms disunite and expose their stigmatic tips to pollination by insects (see fig. 302 [10]). If no insects visit the flower the style-branches roll back and bring their tips into contact with the pollen on the stylar column (see fig. 302 [11]). In all the species that have been examined (*Phyteuma confusum, P. hemisphæricum, P. Halleri, P. orbiculare, P. spicatum*) the style-branches are wound into from 1 to 2 complete coils. In the case of *Phyteuma Halleri* the further observation was made, that after the accomplishment of autogamy the transparent hairs on the stylar column and the pollen adherent to them rapidly dry up, whilst the branches of the style unroll again.

Of the Gentians, the little *Gentiana prostrata*, which grows on the mountains in the vicinity of the Brenner Pass in Tyrol, affords a striking example of the phenomenon in question. The flowers are protandrous; the anthers in the bud are contiguous to the short style and closed stigma, and, when they open, their pollen is deposited upon those organs. Upon the expansion of the corolla, the pollen is available for other flowers through the agency of insects. Somewhat later the stigmatic lobes part, and if after this insects visit the flower, they brush against the receptive spots of the stigma, and may dust them with extraneous pollen. Lastly, the two stigmatic lobes curl back until the receptive tissue upon their upper surfaces reaches the residue of pollen still sticking to the short style.

Much less common modes of operation are for the revolute stigmas to take the pollen from the edge of the tube of connate anthers, from hairs on the corolla, from bristles on the pappus, or from depressions in the petals. The case of abstraction of pollen by stigmas from the edge of the anther-tube I observed in several Composites, as, for instance, in the species of the genera *Adenostyles* and *Caealia*, and in *Arnica montana*. The external surface of the style in *Adenostyles* is beset with papillæ, which give it the rough glandular appearance whence it derives its name of Adenostyles (=glandular style); it has no collecting-hairs, and the pollen is therefore not swept but squeezed out of the anther-tube. The edge of the tube is furnished with prongs, each of which is slightly revolute and is concave almost to the extent of being boat-shaped, so that it is able to retain some of the extruded pollen. This pollen is only used for autogamy in the event of the stigmas not being dusted in any other way. In that case the two style-branches roll back until the receptive tissue comes into contact with the edge of the anther-tube. The style-branches in *Arnica montana* (see figs. $303^{1, 2, 3, 4, 5, 6}$) have collecting-hairs on the surface of their slightly-thickened tips only, and in this case the pollen is regularly swept out (figs. 303^{1} and 303^{4}). A small quantity of the pollen is always left behind upon the 5-toothed edge of the anther-tube. The manner in which the pollen is transferred to the stigmatic tissue by means of the re-volution of the style-arms is shown in the accompanying figure 303^{6}.

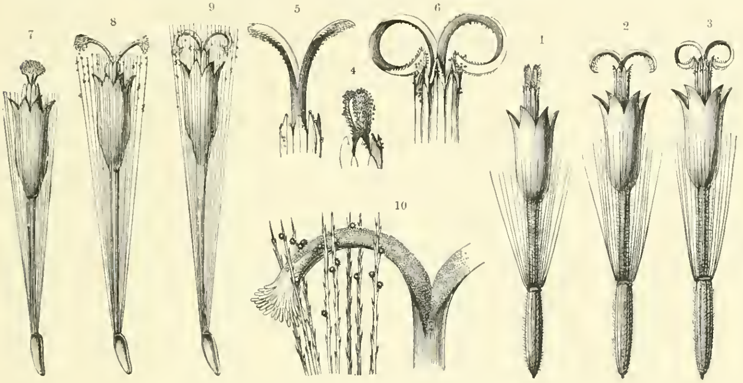


Fig. 303.—Autogamy effected by means of an inflection of the style-branches.

$^{1, 2, 3}$ Flowers of *Arnica montana* in successive stages leading to autogamy. ^{4} Style-branches of *Arnica* in contact shortly after their extrusion from the anther-tube. Pollen is clinging to the collecting-hairs and to the mouth of the tube. ^{5} The style-branches projecting still further from the tube and diverging from one another. ^{6} The style-branches curved back so as to bring the stigmatic tissue into contact with the pollen sticking to the tube of anthers. $^{7, 8, 9}$ Flowers of *Senecio viscosus* in the successive stages of development leading to autogamy. ^{10} A revolute style-branch of *Senecio viscosus* with its stigmatic tissue in contact with the pollen sticking to the bristles of the pappus. All the figures magnified.

As illustrations of the abstraction of pollen from the hairs of the corolla we may take a campanulate, a labiate, and two caryophyllaceous species. The corolla of the Nettle-leaved Bell-flower (*Campanula Trachelium*) has a thick coating of hairs on its inner surface. In the bud these hairs are directed horizontally towards the axis, and touch the style and the anthers. The deposition of the pollen upon the stylar column takes place in the same way as it does in the Bell-flowers already discussed (see p. 361), but the moment the anthers are retracted some pollen is invariably caught by the hairs of the corolla, and when the flower opens a portion of the pollen is always to be seen adhering to them. The humble and hive bees which visit the flower may, of course, bring about cross-fertilization, just as they do in the other Bell-flowers. The style-branches in *Campanula Trachelium* do not, at the close of the flowering period, roll back so far as the central column; a less degree of bending is here adequate to bring the receptive tissue on the tips of the style into contact with the pollen sticking to the hairs.

In *Dianthus neglectus*, a species of Pink indigenous to the Southern Alps, and in the Glacier Pink (*Dianthus glacialis*), the laminæ of the petals are beset with hairs. The pollen is first exposed to the chance of dispersal by insects, but afterwards the stamens curve outwards, and some of the pollen becomes affixed to the hairs of the petals, which usually receive in addition a small deposit as a result of the scattering action of insect-visitors. The flowers are protandrous. The stigmas, which are situated in front of the entrance to the floral interior, wait till the period of the flower's bloom is nearly at an end, for the chance of being touched by insects bearing extraneous pollen. But sometimes no insects come, and in that case the pollen stored upon the hairy laminæ of the petals is made use of at the last moment. The transparent papillose stigmas wind themselves into the shape of the letter S, and, sweeping like a brush over the petals, collect the pollen from them. This operation is materially assisted in both the Pinks under discussion by the fact that the laminæ of the petals grow some millimetres longer during the flowering period, the result of which is to bring the hairs besmeared with pollen a little nearer to the stigmas. In *Dianthus neglectus* there is besides an involution and uprising of the laminæ in the evening, which, likewise, assist the process of sweeping up the pollen by the stigmas.

In *Ballota nigra*, a Labiate with protandrous flowers which grows commonly in hedges on cultivated land, some of the pollen falls at the very commencement of the flower's bloom upon the hairs clothing the borders of the upper lip. If no pollen is brought by insects to the stigma of a flower of this plant, the lower style-arm bends down at the end of the flowering period and takes up the pollen from the hairy mantle above referred to. The same kind of thing happens in a few other Labiates, as, for instance, in *Salvia viridis*, of the Mediterranean flora, whose style bends down in the event of a failure of insects, and brings the stigma into contact with a store of pollen resting upon the under-lip, where it fell at the very commencement of the flower's bloom. I have hitherto observed only in the cases of *Tozzia alpina* and *Pyrola media* the phenomenon of a style curving down to take pollen from cup-shaped hollows in the corolla in which it has lain stored, but it probably occurs in many other plants besides.

The curious case of the pollen being taken from the hairs of the so-called pappus by the stigma is illustrated in figs. 303 7, 8, 9, 10. In the Stinking Groundsel (*Senecio viscosus*), which will serve for an example, the style-branches are furnished at the tips only with bunches of collecting-hairs. As the style elongates these hairs sweep the pollen out of the tube of anthers and leave it in a round lump at the top of the tube (see fig. 303 [7]), whence it may be carried off by insects. At this stage the corolla and the hairs of the pappus are 6 mm. long. Soon afterwards the two style-branches, which have undergone rapid elongation, part asunder, and the pollen, if not already removed by insects, is shaken off, and falls on to the pappus-hairs, where it is caught by the asperities on their surfaces (see fig. 303 [8]). The receptive tissue on the inner faces of the style-branches, which are now the upper surfaces, are in a position to get dusted with pollen brought by insects from other flowers. Meanwhile an elongation of every part of the flower has taken place; the pappus-hairs have attained a length of 7 mm., and the corolla of 6·5 mm. Lastly, the flower enters upon its third stage of development. The two style-branches curve down, bringing the stigmatic tissue into contact with the pollen sticking to the pappus-hairs, which have by that time grown another millimetre, and are therefore reached all the more easily, as they even project above the arms of the style (see figs. 303 [9] and 303 [10]).

In all the cases hitherto dealt with the only parts of the flower which are concerned in bringing about autogamy are the stamens and pistils. The filaments in some instances, the parts bearing stigmatic tissue in others, undergo inclination or inflection, whilst sometimes both organs mutually approach one another. No direct part in the process of autogamy is taken in any of these plants by the whorls of petals surrounding the stamens. We will now proceed to describe cases in which the petals are instrumental in effecting self-fertilization.

The simplest case of the discharge of this function by *petals* is to be found in flowers which are in the shape of tubes, cups, or basins, and whose anthers are adnate to the inner surfaces of the petals, and are brought into contact with the stigma in consequence of a contraction or closing together of the corolla—*Thymelæa Passerina*, a low shrub belonging to the Thymelaceæ, will serve as an example. The small inconspicuous flowers of this species contain nectar, and by its perfume attract insects which brush pollen from the anthers as they suck the honey and convey it to the stigmas of other flowers. The anthers are adnate to the inner face of the cup-shaped perianth, and are at first at a distance of only ½ mm. from the stigmas. Notwithstanding this proximity the viscid pollen is not spontaneously transferred to the adjacent stigma when the flower is first open. It is not till the flower is nearly over that a slight contraction of the upper third of the perianth causes the anthers to be pressed against the stigma, which stands at the same level as themselves. In *Claytonia perfoliata*, one of the Portulaceæ, autogamy is effected in the same manner, the only difference being that the anthers are borne on special filiform filaments which are adnate to the bases of the petals. These filaments, however, share in all the petals' movements, and the anthers at their extremities are pressed exactly upon the stigma when the corolla closes up.

In other cases the epipetalous stamens hold their anthers at the commencement of the flowering period underneath or behind the stigmas, and are pushed upwards during the flowering period by an elongation of the petals, in consequence of which they rest in the last stage against the lateral edges of the stigmas. This process is very common in plants of the order Solanaceæ (*Hyoscyamus, Lycium, Nicotiana, Physalis, Scopolia*), and it has also been observed in Gentianaceæ (e.g. *Erythræa pulchella, Gentiana campestris, G. glacialis*). In some of these plants the elongation undergone by the corolla-tube is very considerable as compared with the size of the flower. In the American Tobacco plant (*Nicotiana Tabacum*) it amounts to nearly ½ cm., whilst in the little Centaury (*Erythræa*) it is only 2 mm. The elongation of the corolla-tube is accompanied in most instances by a stretching of the filaments. In consequence of this combined growth the anthers are, in the case of the short-styled flowers of *Lycium barbarum*, raised ½ cm. in 24 hours. In the Henbane (*Hyoscyamus niger*) the anthers are 7 mm. lower than the stigma in the morning when the flower is nearly open, but by the evening of the same day the simultaneous elongation of the corolla-tube and of the stamens adnate to it has raised the anthers to the level of the stigma and pressed them upon it. It is scarcely necessary to mention that in these plants, which are all protogynous, cross-fertilization is possible in the first part of the flowering period, and it is as a matter of fact very frequently effected through the intervention of insects.

A very curious variety of the phenomenon in question is exhibited by the large-flowered species of the Eyebright genus (*Euphrasia Rostkoviana, E. versicolor, E. speciosa*), and by the allied Yellow Rattles (*Rhinanthus angustifolius* and *R. hirsutus*). The flowers of these plants face sideways, and the corolla has a tri-lobed under lip and a bi-lobed helmet-shaped upper lip. Four stamens of the pollen-sprinkling type, which we have compared to sugar-tongs, are adnate to the corolla-tube. The anthers are concealed beneath the upper lip; the long filiform style is in the shape of the letter **S** and lies above the anthers, and when the flower is first open it projects considerably beyond them (see fig. 277 [4], p. 273). Stigma and anthers are then so placed as to make it inevitable that insects which enter the flower shall first touch the stigma, and the next moment become dusted with a shower of pollen from the anthers. If several blossoms are visited in succession cross-fertilization is certain to take place. If, however, insects stop away, the tube of the corolla elongates and carries up with it the epipetalous stamens. As the style retains its original length, the terminal stigma, which hitherto has projected in front of the anthers, now rests by the side of the anthers or just above them. Thus the stigma is in a sense overtaken by the anthers. In the large-flowered species of Eyebright the tense style then presses upon the anthers, forces them asunder, and, sinking down, brings its stigma between the anther-valves, where it cannot fail to get coated with the pollen of which they are still full. In the species of Yellow Rattle above mentioned, the stamens become flaccid towards the end of the flower's period of bloom and the pollen falls out and is left sticking to the hairs of the anthers or to the involute folds of the corolla, so that the style in brushing by usually removes it.

It is much less common for the *calyx* to play this part in bringing about autogamy. *Tellima grandiflora*, a North American Saxifragacea, is the only case known at present in which the stigma after being at first rather higher than the anthers is overtaken by them and besmeared with pollen owing to an elongation of the calyx and consequent raising of the stamens, which are adnate to the tube of the calyx.

In many plants autogamy depends upon the fact that as the corolla falls off, its tube slips over the stigma, so that the latter rubs against the anthers, which are still laden with pollen, or against the inside of the corolla, which is also besmeared with that substance. This process presupposes that when the flower is in full bloom the anthers are overtopped by the stigma, and that the latter is still in a receptive condition at the time the corolla becomes detached and drops. Both these conditions are as a fact fulfilled in all plants of this category. In the species of the genus *Gilea* (Polemoniaceæ), and in the Brazilian plant *Psychotria leucocephala* (Rubiaceæ), the long filiform styles branch into divergent arms, which bear the delicate stigmatic tissue; and at the period of full bloom, these style-arms project far above both the limb of the corolla and the anthers. Consequently, insects alighting on these flowers encounter first of all the stigmas, and if they are laden with foreign pollen they occasion cross-fertilization. There is, on the other hand, in this form and position of the stigmas the further advantage, that, in case of a dearth of insect-visitors, the stigma may still acquire a supply of pollen when the corolla falls off—that is, at the very last moment of flowering. It is not unusual in these plants to see the corolla, after it has become detached, hanging for quite a long time from the long style and divergent stigmas, and this delay in the process of severance must materially assist the accomplishment of autogamy. The detached corolla persists in a similar manner in flowers with capitate, or short-lobed stigmas, as, for instance, in *Rhododendron hirsutum*, in *Digitalis*, *Anchusa*, *Cestrum*, and various other Scrophulariaceæ, Boraginaceæ, and Solanaceæ. In the case of *Rhododendron hirsutum*, as the corolla slips along the style, the stigma brushes off the pollen, which has invariably been discharged from the anthers before the flower opens and been caught upon the hairs in the interior of the corolla-tube. In *Cestrum aurantiacum*, the anthers, which are borne upon stiff and slightly-inflexed filaments, are pressed against the style, and the corolla is left hanging from the style, usually for a couple of days after its detachment, and does not fall till after fertilization has taken place, when the style also drops off. A great variety of contrivances exists with the object of promoting this method of autogamy by means of a falling corolla. A brief account of three of them will now be given. The flower of the Moth Mullein (*Verbascum Blattaria*), which may be taken as the type of a large number of flowers of Scrophulariaceæ, has a corolla with a very short tube and the limb spread out at right angles to it (*rotate*). Adnate to the tube are five stamens clothed with woolly hairs of a violet colour. The three upper stamens are a little shorter than the two lower ones, and all of them project obliquely beyond the limb of the corolla. The central style is still further exserted, and serves as a perch for insects to alight upon. It is obvious that so long as the parts of the flower are disposed in this manner every insect which arrives with a supply of pollen must effect cross-pollination. As in so many other cases, autogamy is reserved for the last moment of bloom. With a view to its ultimate achievement, the two longer filaments cross themselves over the mouth of the corolla-tube in somewhat the same attitude as a pair of folded arms. This brings their two anthers, which are still full of the orange-coloured pollen, behind the stigma. The corolla now becomes detached from the receptacle and falls forward, but remains for a short time suspended to the long style, where it undergoes slight torsion. Finally, it drops with a gyratory motion, and as it does so the stigma must inevitably be brushed by one or other of the anthers lying in front of the mouth of the flower. The Pimpernel (*Anagallis*), which belongs to the order Primulaceæ, has a corolla resembling that of the Moth Mullein in being rotate and in containing five stamens clothed with violet hairs. The stamens in this case are very long, and the style is bent to one side, and passes between two of the stamens. Thus the stigma is out of reach of the anthers, and cannot, in the first stage of the flower's development, be dusted with their pollen. On the other hand, cross-fertilization may be effected by the small insects which creep over the flat limb of the corolla in order to feed on the hairs of the stamens. The flowers of the Pimpernel belong to the category of those in which the corolla opens and shuts periodically. The operation of closing is due to the expanded limb being thrown into superincumbent folds. On the second occasion of the flower's closing, the anthers come into contact with the part of the corolla that is folded in, and leave some of their pollen sticking to it. This pollen is still to be seen adhering to the inner face of the corolla on the following day, when the limb expands again, and there it remains till the evening, when the corolla closes for the third time. After this the corolla does not open any more, but falls off still closed, and, as it does so, brushes the style, which is held between two stamens, and leaves upon the stigma the pollen that was sticking to its inner surface. Again, there is the case of *Soldanella alpina*, to which we have already several times had occasion to refer in other connections, and also as affording an instance of a second form of autogamy (p. 333) besides that now in question. The style stands up in the form of a column in the middle of the bell-shaped corolla, and has the five stamens close to it. The anthers are united into a cone, and act as sprinklers in the dispersion of their pollen. When an insect pushes into a flower it rubs first against the stigma, and dusts it with foreign pollen, and as it forces its way further in it displaces the various parts composing the cone of anthers, and is consequently besprinkled with pollen. If no insects visit the flower the anthers are still full of pollen when the time comes for the corolla to drop off, and as the style is drawn through the dislocated cone of anthers, the pollen in the interior of the latter is caught up by the stigma, and self-fertilization is effected.

Next to these plants, in which autogamy takes place on the fall of the corolla owing to its tube slipping over the stigma, there comes a group of species in which the same result is attained in the following manner. At the time when the flower opens, the petals are slightly smeared with pollen, and this deposit forms a reserve store. Should the stigma not have received any pollen from extraneous sources, the flower being nearly over, certain movements are undergone by the petals which result in the transference of the pollen sticking to their surfaces, margins, lobes, or folds, as the case may be, to it. The instances of this mode of effecting autogamy are very numerous, and it will be best to class them in small sub-groups, and to take a well-known example from each as an illustration.

In *Argemone, Hypecoum,* and *Specularia,* which will serve as types of the first group, there is no considerable elongation of the pollen-flecked petals during the period of the flower's bloom. This period is only a single day in the case of *Argemone,* and the process takes place in a very simple manner. In the morning, as soon as the petals are wide open and the tension of the sheaf of stamens surrounding the pistil is somewhat relaxed, there is an immediate fall of pollen on to the concave surfaces of the petals (see fig. 304[1]). The flowers are erect, as also is

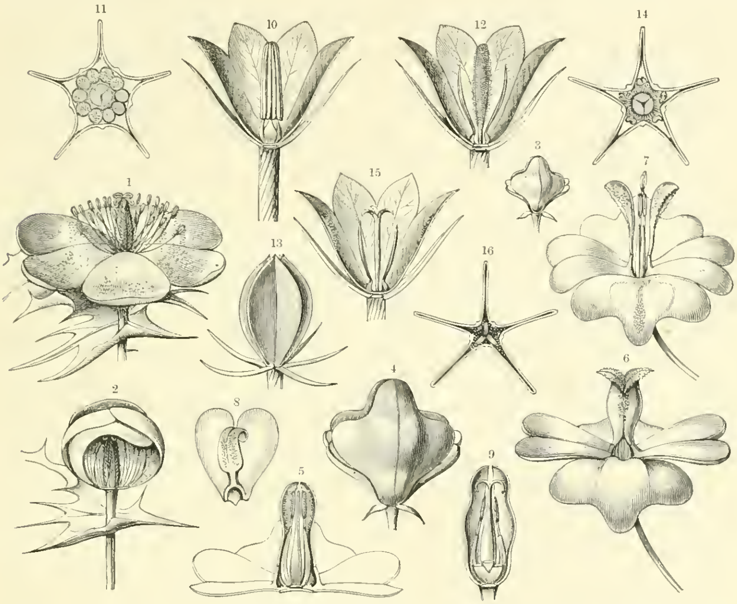


Fig. 304.—Autogamy effected by the petals.

[1] Flower of *Argemone Mexicana* open in the sunshine. Pollen which has fallen from the anthers is resting upon the concave petals. [2] The same flower closed; one of the petals besmeared with pollen is laid upon the stigma; the front petal is removed. [3] Closed flower of *Hypecoum grandiflorum,* natural size. [4] The same magnified. [5] Longitudinal section through the open flower in the first stage of development. [6] Open flower in which the pollen-laden lobes of the inner petals are beginning to separate. [7] The same flower at a later stage. [8] One of the two inner petals; the middle lobe is coated with pollen; at its base is the pit containing the honey. [9] Longitudinal section through a closed flower in its last stage of development. [10] *Specularia speculum*; longitudinal section through an open flower in the first stage. [11] Transverse section through a closed flower in the first stage. [12] Longitudinal section through an open flower in the second stage. [13] Closed flower. [14] Transverse section through a closed flower in the second stage. [15] Longitudinal section through an open flower in the last stage. [16] Transverse section through a closed flower in the last stage. [1], [2], [3] natural size; the rest magnified.

the pistil, and the stellate stigma, which offers the best alighting place for insects, rests at a slightly higher level than the anthers, and at a sufficient horizontal distance from them to prevent their pollen from reaching, spontaneously, its receptive tissue. In the course of the day insects arrive with pollen from other blossoms and cause cross-pollination. When the evening comes the petals close up over the pistil, and one of them brings its inner surface, which is covered with pollen, into direct contact with the stigma (see fig. 304 [2]).

The case of the *Hypecoum* is far more complicated. The flowers of this plant have two small sepals and four large tri-lobed petals (see figs. 304 [3] and 304 [4]). The latter are arranged in two pairs at right angles to one another, one pair being inserted a little higher than the other. The middle lobe of each of the petals belonging to the upper pair is curiously modified; its surface is concave, and in the young flower has the shape of a spoon with fringed edges. The function of these lobes is to collect all the pollen from the anthers at the very commencement of flowering. The anthers are, like those of Compositæ, coherent into a tube inclosing the style; but instead of opening inwards as the latter do, they are extrorse, *i.e.* dehisce outwards. At the time of dehiscence and of the discharge of the pollen the two spoon- or pouch-shaped central lobes of the upper petals are in close proximity to the anthers, and they receive the whole of the pollen (see fig. 304 [5]). After this transfer has been accomplished the two lobes now containing the pollen separate from one another, the first parts to disunite being the free extremities at the top, then the lateral edges (see fig. 304 [6]). The pollen is thus exposed and may be carried off by insects which come for the honey concealed in a little depression at the base of each lobe (fig. 304 [8]). The two linear stigmas being in close contact at this stage, their tissue is not as yet accessible; they do not disunite till two days after the first opening of the flower, but when that interval has elapsed they diverge, and then constitute the most convenient place for insects to settle upon. They are now in exactly the same position as was previously occupied by the pollen-laden lobes (see fig. 304 [7]), and therefore if an insect alights upon them after visiting younger flowers, it is sure to dust the stigmatic tissue with foreign pollen. Meantime the petal-lobes which received the pollen become much more reflexed, especially at their lateral edges; the back of each lobe, which was originally convex, is now deeply concave like a boat, and the whole structure is in a manner turned inside out. The direction of the two divergent stigmas is at right angles to the two upper petals, and their tips point towards the median line of the two outer ones. In consequence of this arrangement the stigmas are at such a distance from the pollen on the lobes that no autogamy could take place without some special intervention. The requisite assistance is afforded by the two outer or inferior petals, and their mode of action is as follows. When evening comes the flower closes; the two lateral pollen-free lobes of each superior petal rise up first of all, and then the two inferior tri-lobed petals wrap themselves over them (see figs. 304 [3] and 304 [4]). On the second or third day, when the margins of the pollen-laden lobes have curled back, contact ensues between the two closed petals and the revolute margins of these lobes, and some of the pollen sticks to the petals, so that next day when the flower opens again a streak of pollen may be seen along the middle line of each of the outer petals (see fig. 304^{7}). On the last day of bloom the two stigmatic arms curve down, and when the flower closes once more at dusk, they, being directed towards the median lines of the outer petals, are brought into contact with the pollen adherent along those lines (see fig. 304^{9}), and thus at the last moment autogamy is effected.

The flowers of the Venus's Looking-glass (*Specularia speculum*, see figs. $304^{10, 11, 12, 13, 14, 15}$) are protandrous like those of the common Bell-flower (*Campanula*); their anthers form a tube in the newly-opened flower (see figs. 304^{10} and 304^{11}), dehisce inwards and deposit the whole of their pollen on to the delicate hairs which clothe the external surface of the stylar column. When the tube of anthers breaks up through the shrivelling of their empty lobes, an axial column covered with pollen is exposed to view, and is used by insects as an alighting place. For the present pollen can only be taken away—not deposited—by insects, for the style-arms are still united, and the receptive tissue is inaccessible. Every evening the erect basin-shaped corolla folds up longitudinally in such a manner as to form five re-entrant angles (see fig. 304^{13}). The in-folded angles of the corolla reach inwards as far as the central column (see fig. 304^{14}), and get besmeared with some of the pollen with which it is coated. The next morning when the corolla opens linear streaks of pollen may be seen upon its internal surface. Meanwhile the three short arms of the style have disunited and spread themselves out, whilst the pollen has fallen off the stylar column (see fig. 304^{15}), or been carried away by insects. If at this stage insects alight on the divergent style-arms fresh from visiting younger flowers, cross-pollination is certain to ensue. As night approaches the flower closes in the same way as on the previous evenings, and the pollen sticking to the lines of the internal folds comes against the style-arms, which are spread out and slightly reflexed (see fig. 304^{16}), and thus effects self-pollination. In the event of the stigmatic tissue having already received a deposit of foreign pollen, this act of self-pollination is superfluous, but otherwise the process is effectual, and always results in the formation of fruit. A similar phenomenon may be observed in the nodding or pendent flowers of various Solanaceæ, particularly in the Potato plant (*Solanum tuberosum*), for here also there is frequently a transference of pollen to the corolla, and from the folds of the corolla to the stigma. But in this case the pollen issues from the anthers through terminal pores, and falls irregularly and not necessarily upon particular parts of the corolla, so that autogamy is not so certain to take place in these plants as in *Specularia*.

From the above descriptions it will be seen that in *Argemone*, *Hypecoum*, and *Specularia*, although the corolla is the part of the flower which is instrumental in effecting autogamy, the process does not involve any noticeable elongation of the pollen-besmeared corolla during the period of flowering. We have now to deal with another group of plants in which the petals perform just the same function as in the foregoing cases with respect to autogamy, but in which a very important part of the operation consists in an elongation of the corolla. Types of this group are afforded by Gentianaceæ of the subdivision Cœlanthe (*Gentiana asclepiadea, G. Pneumonanthe,* &c.), Liliaceæ (*Colchicum*), Amaryllidaceæ (*Sternbergia*), Iridaceæ of the genus *Sisyrinchium,* and those Composites whose capitula are furnished with ligulate florets (*Crepis, Hieracium, Hypochæris, Leontodon,* &c.).

Gentiana asclepiadea (see fig. 305) is one of the sub-alpine species of the Baltic flora, and has protandrous flowers. The anthers are united into a tube, as in the case of Composites and Bell-flowers. They do not, however, discharge their pollen into the tube, but behave in this respect in the same manner as those of *Hypecoum,* that is to say, they open by longitudinal fissures down their external faces, so that after dehiscence the outside of the anther-tube is covered all over with pollen (see fig. 305^{3}). The linear style-branches bearing the stigmatic tissue are at this stage closely united and as yet immature. Humble-bees are attracted in large numbers by the rich store of honey in the floral interior, and as the funnel-shaped corolla is wide open in the daytime the insects enter, and are often entirely engulfed in the flower. If the visit is paid to a young, newly-opened flower the insect loads itself with pollen by coming into contact with the tube of anthers. Two days later the linear stigmas separate and curve over downwards. Their position now renders it inevitable that they should be touched by the bees, of which a large number continue to visit the flower, there being still plenty of honey in it. If these visitors have recently visited younger flowers they are sure to effect cross-fertilization. The corolla is disposed in peculiar folds, as is shown in figs. 305^{1} and 305^{2}; to describe them sufficiently briefly for our present purpose would not be possible. When the flower expands in the morning these plaits open out; at sunset they are again drawn in towards the middle of the funnel, and at the same time a movement

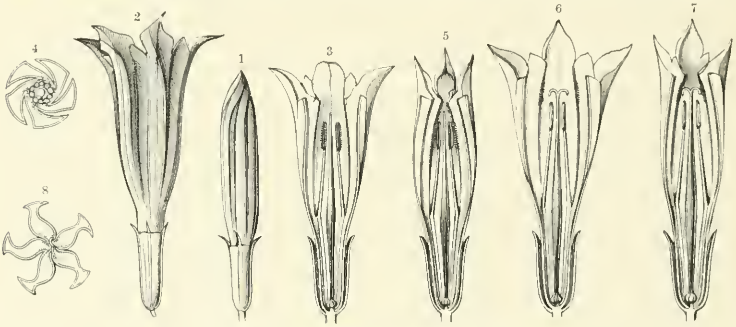


Fig. 305.—Autogamy effected by means of the corolla.

^{1} *Gentiana asclepiadea.* Flower-bud shortly before it opens for the first time. ^{2} Open flower in the last stage of development. ^{3} Longitudinal section through a flower which has just opened for the first time. ^{4} Transverse section through the same flower. ^{5} Longitudinal section through a flower closed for the first time. Pollen is affixed to the edges of the folds into which the corolla is thrown. ^{6} Longitudinal section through a flower which has opened for the last time. ^{7} Longitudinal section through a flower which has closed for the last time. The pollen is being transferred from the folds of the corolla to the reflexed stigmas. ^{8} Transverse section through the same flower. The anther-tube in ^{3}, ^{5}, ^{6}, and ^{7} is represented in optical section.

of torsion takes place which brings the folds into the position shown in transverse section in fig. 305 [4]. The re-entrant angles come into direct contact with the surface of the anther-tube (see figs. 305 [4] and 305 [5]) and take from it some of the pollen, which is very adhesive. On the next day, and on the third and fourth days, the flower opens and shuts again. During that time almost every part of the flower grows in length; the filaments gain 1 mm., the pistil 3 mm., and the inferior half of the corolla as much as 5 mm. In consequence of this growth the pollen transferred to the folds of the corolla from the anther-tube is raised 5 mm., and rests at the same level as the stigmas, which have in the meantime become divergent. When darkness sets in, and the corolla once more falls into folds and closes up, the pollen affixed to the re-entrant angles is transferred to the stigmatic tissue. The process is greatly facilitated by the fact that, at this final stage of flowering, the internal folds assume a somewhat different form and position (see fig. 305 [8]), for in consequence of this change the parts besmeared with pollen are brought still nearer to the middle of the flower. This marvellous contrivance for promoting autogamy may also be observed in *Gentiana Pneumonanthe*, a species which grows in damp meadows in England and all over the continent of Europe, and in this instance the elongation of this funnel-shaped portion of the corolla in the interval between the first and last occasions of the flower's closing amounts to some 7 mm.

The phenomenon occurs in a much simpler form in *Sternbergia* and *Colchicum*, belonging to the orders Amaryllidaceæ and Liliaceæ respectively. The flower of *Sternbergia lutea* has an erect funnel-shaped perianth composed of six segments, three of which are rather longer than the other three. The six upright stamens have nectar secreted at their bases, and are adnate to the segments of the perianth; they are arranged in two whorls round the styles, and have their anthers turned outwards. The styles rise up in the middle of the flower in the form of three long threads. The stigmas, in which the styles terminate, are higher than the anthers throughout the period of bloom, and as, after the dehiscence of the anthers, the pollen adheres to the internal walls of the loculi, it is not spontaneously transferred to the stigmas in the same flower. The flowers are protogynous, and at the commencement of their bloom are adapted to cross-pollination through the agency of insects. Even after the extrorse anthers have dehisced, insects entering the blossom in quest of honey brush first against the stigmas, and only subsequently come into contact with the anthers resting at a lower level. The perianth is open in the daytime alone; in the evening its segments close together so tightly that their inner surfaces touch the extrorse anthers and become smeared with pollen. This happens the very first evening following on the dehiscence of the anthers. The pollen affixed to the perianth-segments does not reach the level of the stigmas till the following day. Its ascent is due to an elongation of the lower regions of the perianth-segments. There is a simultaneous growth of the other parts of the flower, but it is surpassed by the extraordinary increase in the length of the perianth-leaves. Whilst the styles grow 4 mm., and the stamen-filaments from 9 to 10 mm., these segments grow 18·5 mm. Afterwards, when the perianth closes for the night, the pollen is transferred from the inner faces of its segments to the stigmas. Two subsidiary circumstances co-operate in bringing about this act of autogamy. The first is, the fact that the free extremities of the styles which bear the stigmatic tissue curve outwards when the flower's end approaches, and the second is, the circumstance that the excessive elongation is especially marked in the three perianth-segments which are opposite the stigmas.

The same events take place in the flowers of the Meadow Saffron (*Colchicum autumnale*). Anyone crossing a meadow in the autumn in which this plant is growing may see what a great difference exists between young and old flowers in respect of the length of the perianth-segments, and can easily convince himself of the connection between this diversity and the operation of autogamy as explained above. In the Meadow Saffron the phenomenon is somewhat complicated by the circumstance that heterostylism (see p. 302) plays a much more important part in this instance than in the other Liliaceæ. *Colchicum* possesses long-styled, mid-styled, and short-styled flowers, which all grow promiscuously together in one and the same meadow, and the elongation of the perianth-segments is anything but uniform in these three forms. Careful measurements of some five hundred specimens gave the following remarkable result. In long-styled flowers the three longer perianth-segments grow 9 mm. and the three shorter 12·6 mm.; in short-styled flowers the longer segments grow 10 mm. and the shorter 15 mm., and in the mid-styled flowers the longer segments grow 13·5 mm. and the shorter 18·5 mm. I shall return to the subject of heterostylism again presently, and shall then have an opportunity of entering more fully into its significance; at present it is only necessary to mention that the stigmas of the short-styled flowers, when the latter are nearly over, come into contact not only with the pollen sticking to the perianth-segments, but also with the tips of the anthers themselves, for in this form there is a proportionate growth of the filaments.

This same process, which in *Colchicum autumnale*, in Sternbergias and in Gentians of the Cœlanthe tribe only culminates in autogamy after the lapse of a week, is accomplished in the delicate plant *Sisyrinchium* of the order Iridaceæ in the course of a few hours. Apart from their ovaries, which are inferior, the flowers of *Sisyrinchium* are constructed similarly to those of Liliaceæ. The three small petaloid stigmas, in which the styles terminate, project above the anthers. The latter are coherent into a tube and open extrorsely, whilst the flower is still in the bud state, and the consequence is that some of their pollen is affixed to the contiguous leaves of the perianth. The flower opens out into a cup, and insects may then cause heterogamy; but on the approach of evening the perianth closes again, and autogamy takes place owing to the fact, that in the course of those few hours the petals have lengthened exactly enough to bring the pollen sticking to their inner surfaces to the level of the stigmas.

Reference must also be made to those Composites in which autogamy is brought about by means of an elongation of the ligulate corolla, and the consequent uplifting of the pollen adherent to it. In most and probably in all species of *Crepis*, *Hiera-*

cium, *Leontodon*, and *Hypochæris*, in whose capitula the peripheral ligulate florets are considerably longer than those of the centre, it is easy to see that when the capitula close in the evening the ligulate petal in each flower rises up and lays its inner surface upon the pollen which has been extruded from the tube of anthers in the course of the day. The pollen remains sticking to the petal during the two succeeding days, and in the meanwhile the latter grows about a couple of millimetres in length and carries the pollen up with it. At the same time the style undergoes elongation and protrudes out of the top of the tube of anthers, holding its two arms, which are now divergent and expose the receptive stigmatic tissue upon their surfaces, at the same level as the pollen sticking to the ligulate corolla. When next the capitulum closes, the pollen is transferred to the stigmas, and autogamy ensues. This adaptation of the marginal florets of the capitula is all the more interesting, seeing that in the central florets in the same plants, geitonogamy has been found invariably to prevail (*cf.* p. 319).

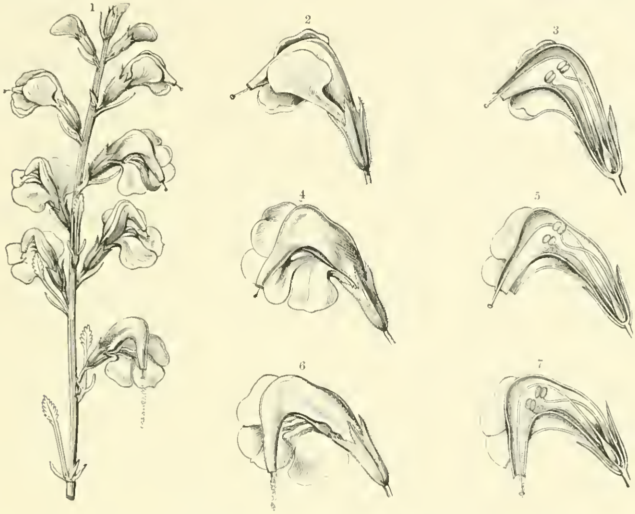


Fig. 306.—Autogamy effected by means of the corolla.

[1] *Pedicularis incarnata.* [2] A flower of *Pedicularis incarnata* which has just become accessible to insects. [3] Longitudinal section through the same flower. [4] The same flower in a later stage of development. [5] Longitudinal section through the flower of [4]. [6] The same flower shortly before the corolla fades; the upper lip is bent down and the mealy pollen falling out of the loosened valves of the anthers is trickling through the tubular upper lip upon the stigma stationed in front of the mouth of the tube. [7] Longitudinal section through the flower of [6]. [1] nat. size; the other figures double their nat. size.

One of the most curious contrivances for effecting autogamy consists in a special inflection of the corolla, on the termination of the flower's period of bloom, enabling it to conduct the pollen which falls from the anthers to the stigmas. The pollen in these cases is of mealy consistence. Two species of the Lousewort genus (*Pedicularis*) may be used to illustrate this form of adaptation, and we will first take

Pedicularis incarnata (see fig. 306), a species which grows abundantly in Alpine meadows. The flowers of this plant are arranged in spikes, and their development proceeds from below upwards (fig. 306^{1}). The corolla is bilabiate; the lobes of the under lip are at first upturned (see fig. 306^{2}), but subsequently are expanded in a slanting plane (figs. 306^{4} and 306^{6}). The upper lip is helmet-shaped and rolled into a tube at the apex (figs. 306^{2,3,4,5,6,7}). The stamens are of the sugar-tongs type, and their anthers are concealed underneath the arch of the upper lip (figs. 306^{3,5,7}). The long style is bent at an angle to correspond to the form of the upper lip; its anterior extremity passes through the tube and rests in front of the orifice and at the same time in front of the entrance to the floral interior. The humble-bees which make use of this entrance are obliged to rub against the stigma, and if they come laden with pollen from other flowers cross-fertilization ensues. Owing to the fact that the flowers are protogynous insect-visitors cannot, in the first stage of bloom (figs. 306^{2} and 306^{3}), carry off any pollen, but can only leave behind upon the stigma what they have brought with them; at later epochs, however, the insects, though still brushing first against the stigma, are next moment besprinkled with the mealy pollen which falls from the anthers in consequence of the disturbance of the tongs-like stamens. Under the galeate arch of the upper lip there is a slit (fig. 306^{4}) to allow the pollen to fall freely, and whenever an insect enters between the under and upper lips this gap is enlarged. The head is the part of the humble-bee that receives the pollen, and the latter may, of course, then be conveyed to other flowers. If no insects visit a flower, the pollen remains for rather a long time dormant in the anthers; but, in the last stage of bloom, the filaments become flaccid and give way, and the pollen then falls of itself upon the edges of the slit. At the same time the upper lip undergoes a marked downward bending (fig. 306^{6}), whereby that part of it which is prolonged into a tube, is brought into a vertical position, so that the pollen rolls down it, and is directed on to the stigma, which hangs right in front of the mouth of the tube (fig. 306^{7}). Sometimes the stigma is drawn into the tube in the process of bending above referred to and sticks there, like a cork in the neck of a bottle; in which case self-pollination takes place inside the tube. Autogamy of the type exhibited in *Pedicularis incarnata* occurs with slight variations in all species which have the upper lip of the corolla produced into a tubular beak. The cases of this kind especially subjected to investigation were *Pedicularis asplenifolia*, *P. Portenschlagii*, *P. rostrata*, and *P. tuberosa*.

Very different behaviour is observed in several species of the same genus in which the upper lip has the form of a cowl or a helmet truncated in front, as, for example, *Pedicularis Œderi*, *P. foliosa*, *P. comosa*, and *P. recutita*. Of these we will take for illustration *Pedicularis Œderi*, which grows abundantly in Alpine meadows in the neighbourhood of the Brenner Pass in Tyrol. As regards the construction of its flowers, this species differs from *P. incarnata* in that the stigma is stationed in front of the truncated helmet forming the upper lip, and also in having projecting ribs on both sides of the corolla, which act like a system of levers in causing the inflection just before the flower fades. The entire upper lip at this stage bends down so sharply as to look as if the flower had been wilfully broken. The back of the upper lip, which originally constituted a direct prolongation of the corolla-tube, now forms with it an angle of 60°, and later an angle of 90°. The movement is shared, of course, by the style and by the tongs-like stamens concealed beneath the upper lip. The consequence is that the stigma at the end of the style is no longer in front of the anthers, but underneath them, and that the anthers, which hitherto have been held tightly together, move asunder and let their pollen fall. The stigma is situated in the line of descent of the pollen, and, being very viscid, it catches a quantity of the particles of the shower, and thus secures the accomplishment of autogamy (*cf.* fig. 276, p. 272). The same changes of position, which, spontaneously initiated at the close of the flowering period lead to autogamy, may, curiously enough, be brought about at an earlier stage by the humble-bees which fasten on to the flower, but in that case they result in cross- and not self-fertilization. For a description of the processes involved the reader is referred to the account of them given on p. 272, where *Pedicularis recutita* is the species dealt with. We may here remark that the whole of the pollen which falls from the anthers in the last stage of flowering is not devoted to autogamy; the few pollen-cells which stick to the viscid stigma are sufficient for that purpose. A larger number of pollen-cells fall past the stigma into the air, where they may be caught up by a gust of wind, and carried away in the form of a tiny cloud of dust. If mature stigmas of other *Pedicularis*-flowers happen to lie in the direction in which the dust-cloud travels, individual cells of the cloud are left behind on these stigmas, and cross-fertilization thus ensues in the same way as in the flowers of the Toothwort (see p. 330).

Of the Rhinanthaceæ most nearly allied to the genus *Pedicularis* a few species of the Cow-wheat, which may be represented by *Melampyrum sylvaticum*, remain to be mentioned as instances of plants exhibiting the form of adaptation above described. The sole difference is that in *Melampyrum sylvaticum* the tube of the corolla bends at a sharp angle at a point only 2 mm. above the base, whilst the limb itself, composed of the lips, undergoes no independent flection. The result is the same as in those species of *Pedicularis* of which an account has been given, inasmuch as the pollen falls, in consequence of the inflection, from the anthers of stamens of the sugar-tongs type on to the stigma beneath.

A kindred process to the preceding consists in the anthers with their coating of pollen being brought into contact with the stigma by means of an inflection of the corolla. The pollen is not mealy in this case, but adhesive. No one who will take the trouble to examine the inflorescence in one of the twining species of Honeysuckle (*Lonicera Caprifolium, L. Etrusca,* or *L. Periclymenum*) can fail to notice that the corolla-tube, in buds which are about to open, ascends in an oblique direction, that in newly-opened flowers it is horizontal, and that, a short time before a flower fades, it is bent downwards. The angle through which the axis of the flower is displaced relatively to the flowering stem varies from 45° to 90°; in the case of horizontal stems it is less, and in that of erect stems greater, but the object invariably aimed at is that the open corolla shall, as night comes on, be disposed in the most convenient manner possible for nocturnal moths to visit it. In flowers adjusted in anticipation of such visits, the stigma takes up a position which precludes the possibility of its being dusted with pollen from the anthers in the same flower. In the act of introducing their long probosces into the honey secreted in the interior of the flower, Sphingidæ come into contact first with the stigma and then with the anthers, and as they travel from flower to flower they are the means of effecting cross-pollination in this as in so many other cases. But should no moths come upon the scene, autogamy invariably takes place through the inflection of the corolla-tube already referred to. The stamens are adnate to the corolla-tube, and undergo inflection with it, thus bringing the anthers, still covered with pollen, into direct contact with the stigma, which, in the horizontal position of the flower, was stationed a little lower than, and in front of, the anthers.

In respect of the manner of their autogamy the last-mentioned plants exhibit a transition to a large group in which self-fertilization is prevented during the early stages of flowering by the relative positions of anthers and stigmas, but is effected towards the end of the period of bloom, when certain changes in the position and direction of the *flower-stalks* have taken place and brought the pollen and stigmas into conjunction. These alterations of position are usually associated with one of the many other contrivances already described. Thus, for instance, the styles or the filaments may undergo elongation and inflection, or the corolla may grow up and carry with it pollen affixed to its petals, or the stamens themselves, and so forth; but these processes would not of themselves be sufficient to induce autogamy if it were not for the part played by the flower-stalks. To put it briefly, the stigmas and the anthers become, in the absence of cross-fertilization, so situated by the growth and inflection of the flower-stalk as to render autogamy inevitable. When we consider that the changes in the position and direction of pedicels, and the consequent drooping or straightening up of flowers, serve other purposes of great importance in the life of plants, and that, in particular, to these inconspicuous movements are often due the protection of pollen from moisture and the placing of the entrance to a flower in the position most convenient to insects whose visits are profitable to the plant, we cannot be surprised to find that this form of adaptation is one of the commonest of all. A combination of advantages, either simultaneous or in rapid succession, is secured, and contrivances of this kind which best contribute to the economy of plant-life are found by experience to be invariably the most widely distributed.

We will first consider flowers in which the stigma begins by being situated outside the line of descent of the pollen as it falls from the anthers—a circumstance which is advantageous inasmuch as it favours cross-fertilization—but where subsequently the entire flower assumes a different position in consequence of a growth or an inflection of the flower-stalk, whilst the direction and situation of stamens, style, and stigmas remain the same as before. In several species of *Narcissus*, *e.g.* the graceful *Narcissus juncifolius*, and in some Boragineæ, such as the common Wood Forget-me-not (*Myosotis sylvatica*), the flowers at first have their mouths set in a lateral direction; the stigma is stationed behind the anthers, and the pollen that falls out of the anthers does not come upon the stigmas so long as the corolla-tube is horizontal. During that period the branch of the inflorescence to which the horizontality of the corolla is due is curved, but it subsequently straightens out and raises the corolla-tube to a vertical position whereby the stigma is brought into the line of descent of the pollen as it falls from the shrivelling anthers. This occurs in *Tulipa sylvestris, Polemonium cœruleum, Saxifraga hieracifolia, Chrysosplenium alternifolium, Rhododendron Chamœcistus, Vaccinium, Arctostaphylos, Cerinthe, Symphytum*, and *Cyclamen*. The process may be most clearly traced in the various species of *Cyclamen*, which are at present so commonly grown in pots. The first day that the flower is open and the petals reflexed, the peduncle, which rises up from the ground, has its extremity bent over almost at a right angle. The short bent piece of the stalk is inclined at an angle of from 50° to 60° to the horizon. The variation in the size of the angle is due to the fact that the longer inferior part usually ascends obliquely from the ground, and is only in rare cases quite vertical. From day to day the angle of inclination may be seen to diminish by about 10° until at the end of the flower's period of bloom the short down-bent portion at the top and the long upright portion of the peduncle are almost parallel, and the whole has the form of a crook. As the style lies in the direct line of prolongation of the short piece of the peduncle and projects beyond both the tube of the corolla and the cone of anthers, autogamy cannot take place in the first stage of the flower's development, when the style is inclined at an angle of from 50° to 60° to the horizon. Insects visiting the flower at this period first brush against the stigma at the end of the projecting style, and may occasion cross-fertilization; but even if it should happen that the displacement of the anthers caused by an insect's intrusion has the effect of letting some of the pollen fall out, the shower does not descend upon the stigma, for it is not yet situated vertically beneath the anthers. Towards the close of the flowering period, on the other hand, the stigma is moved by means of the inflection of the peduncle above referred to into the path along which the pollen descends; the filaments become flaccid, the anthers disunite, and the pollen stored in the cone is sprinkled upon the still receptive surface of the stigma.

This will be the best place to describe the curious case of autogamy which is exhibited by the *Calceolaria Pavonii* of South America. The flowers of this plant are protogynous, and when first open they are borne on almost horizontal stalks. The anthers, which are still closed, are concealed beneath the shortly truncate upper-lip. The style bearing the already mature stigma is borne horizontally, its tip only being bent down like a hook at a short distance from the stigma (as is shown in figs. 307 [1] and 307 [2]) so as just to touch the roof of the inflated under-lip. The short-tongued Hymenoptera which come in quest of the honey secreted within the lower-lip make use of its roof as an alighting-place. The instant one of them settles upon it the lip drops as in the case of the Snapdragon, the movement being regulated by the powerful ribs on each side of the corolla. The result is twofold: the jaws of the flower are set wide open and the honey-secreting lobe hitherto concealed in the hollow of the lip is brought out so as to enable the insect which has caused the movement to lick up the honey without difficulty. In doing so, however, it rubs its back against the stigma, and should it have previously visited older flowers cross-pollination ensues. These are the conditions at the commencement of flowering. The next day or the day after that, the anthers open by comparatively large pores, one at the top of each loculus. The connectives are articulated to the filaments, so that when the latter are pushed the anthers are set swinging and let fall some of their mealy pollen. If under these circumstances a rather large Hymenopter alights on a flower in quest of honey, he must necessarily knock against the filaments and be sprinkled by the pollen which descends in consequence, especially seeing that the filaments have meanwhile increased in length sufficiently to bring the upper lobes of the anthers upon the highest part of the arched external surface of the under-lip. If the flower is not visited by insects, a quantity of the mealy pollen falls of itself upon this convex surface (see fig. 307^{2}). Soon afterwards the flower-stalk curves down, causing a steep inclination of the roof of the under-lip, which still bears on its highest part the heap of pollen deposited by the anthers. The pollen slips down the inclined plane, and is thus brought into contact with the stigma, which still retains its receptive power (see fig. 307^{3}).

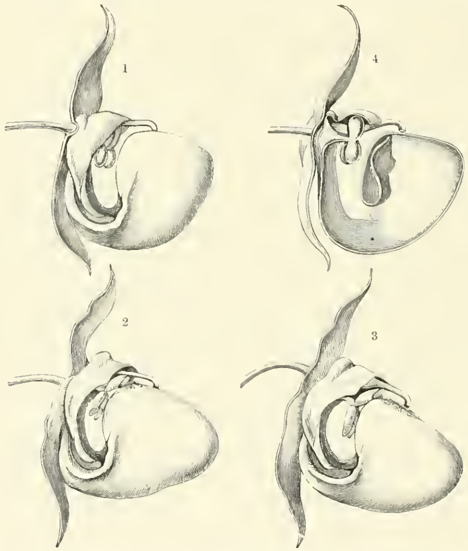


Fig. 307.—Autogamy caused by inflection of the flower-stalk and the adjustment of the under lip to form an inclined plane down which the pollen deposited upon the under-lip slides to the stigma: *Calceolaria Pavonii.*

$^{1, 2, 3}$ Side view of the flower in the three successive stages leading to autogamy. ^{4} Longitudinal section through a flower in the first stage of development. All the figs. slightly magnified.

The acccomplishment of autogamy, by means of a *combination of movements and inflections* of the flower-stalks with similar action on the part of the stamens and style is of as common occurrence as it is varied in respect of details. The drooping Star of Bethlehem (*Ornithogalum nutans*) derives its name *nutans* from the attitude of its flowers, but the latter really do not assume that position until quite at the last; in the bud-stage they are erect, and even after the leaves of the perianth have expanded the pedicels stand out horizontally from the axis of the inflorescence, and the flowers face sideways. The flowers are protandrous. The anthers of the three stamens, situated in front of the little pits in the ovary in which honey is secreted, dehisce at the same moment as the perianth-leaves expand, and these anthers are placed in such a position as to be touched by insects as they enter the flower. The stigma is still immature at this stage. A little later, when the stigmatic tissue has developed the power of retaining pollen, the stamens move out of the way of insects towards the periphery of the flower and thus render it possible for cross-pollination to be effected by such of these visitors as bring with them pollen from younger flowers. In the third stage of the flower's duration the pedicel bends down until the flower is at last truly nodding. The stamens have meantime executed a reverse movement towards the middle of the flower, and the stigma is found to be just underneath one of the anthers belonging to a stamen of the shorter class. These anthers always have some pollen left in them, for they do not open till the second stage of the flower's development and cannot have undergone contact with insects. The gradual shrinkage of the anthers now causes this store of pollen to fall out of them on to the adjacent stigma, and thus autogamy is effected just before the flower fades.

The hermaphrodite flowers of certain Rosaceæ — *Dryas octopetala, Geum coccineum, G. montanum, G. reptans, Potentilla atrosanguinea, P. repens,* and *Waldsteinia geoides*—and those of some Ranunculaceæ, viz., *Adonis vernalis, Anemone alpina,* and *A. baldensis* afford particularly instructive examples of autogamy. In all these plants the flowers are protogynous and are characterized by having a large number of carpels crowded together in the centre and surrounded by equally numerous stamens, which are disposed in several whorls. In the Rosaceæ in question the stamens are tucked down before the bud unfolds, and they do not straighten out until the anthers are nearly ready to open. Dehiscence occurs first in the anthers which belong to the outermost whorl of stamens, and are furthest away from the stigmas of the bunch of ovaries in the middle. This relative position of the two sets of organs excludes all possibility of autogamy, especially when the flower is erect; on the other hand, cross-pollination is quite likely to be effected by insects, which alight on the stigmas, thence proceed towards the circumference of the flower, licking up honey and collecting pollen on the way, and finally take wing from the edge to visit other flowers. By degrees, the stamens of the innermost whorl come to maturity; they straighten out and elongate, and their anthers with pollen exposed upon them are brought to the same level as the stigmas of the central pistils. A transference of pollen to some of these stigmas is now certain to ensue, and is rendered all the more inevitable by the outward inclination and inflection of the styles belonging to the pistils most remote from the centre which now take place, and bring the corresponding stigmas into direct contact with the pollen. But if this were all, the stigmas in the centre might get no share of pollen in the event of an absence of insect visitors. To obviate this possibility the flower-stalk bends in a gentle curve to one side so as to bring the last-mentioned stigmas into the line of descent of the pollen when it falls from the anthers at the end of the flowering-period. The process in the Ranunculaceæ referred to only differs from that just described in trifling respects. In *Adonis vernalis* no outward inflection of the style can take place on account of its shortness, but on the other hand the stamens nearest to the ovaries curve inwards and deposit their pollen upon the adjacent stigmas. In *Anemone alpina* the anthers of the innermost whorl of stamens are the first to open, and the order of development is from that whorl outwards. Owing, however, to the fact that the styles are crowded close together in a dense tuft at that earliest stage, autogamy is not effected at once; later on the styles become bent and twisted, and some of the stigmas touch the anthers in consequence; and when in addition the pedicel undergoes inflection and causes the flower to nod, the rest of the stigmas are brought vertically under the anthers and catch the pollen which falls from them. In *Pyrola uniflora* (see fig. 308^{2}), a native of fir-woods, autogamy is brought about at the close of the flower's period of bloom by means of a marvellous co-operation of the stamen-filaments and the flower-stalks. The bud about to open (see fig. 308^{1}) and the young flower whose petals have just expanded (see figs. 308^{2} and 308^{3}) are borne on stalks which are strongly curved, and they are thus inverted and pendent. The style is vertical, with the stigma pointing downwards. The filaments are **S**-shaped and hold the anthers, which are of the pepper-castor type, with the two pores invariably uppermost so that the pollen does not fall out of itself or at any rate cannot come upon the stigma (fig. 308^{3}). Insects approaching from below brush first against the stigma and directly afterwards against the anthers which are in consequence upset, and besprinkle the intruders with pollen. This pollen is then carried to other flowers of *Pyrola uniflora*, where it is retained by the viscid stigmas and fertilizes the ovules. During the period of bloom two changes are effected, which though not very striking in themselves are yet of extreme importance with a view to autogamy. In the last stage of the flower the curve of the pedicel no longer amounts to a semicircle, and consequently the flower is no longer absolutely pendulous but only facing obliquely down (fig. 308^{4}); the style is no longer vertical, but with this new position of the flower points also obliquely downwards and the stigma is thus brought underneath some of the anthers. The filaments are still curved in the shape of the letter **S** but in the opposite direction to that held by them at the commencement of the flowering-period (*cf.* figs. 308^{3} and 308^{5}); the anthers are therefore inverted and have their pores directed downwards. The least shaking of the slender stem by the wind is now sufficient to cause a fall of pollen, and, in its present position, the viscid stigma cannot fail to get sprinkled with some particles from the shower which descends on such occasions (see figs. 308^{4} and 308^{5}).

In *Phygelius capensis*, a plant belonging to the Scrophulariaceæ of the Cape, and also cultivated elsewhere in gardens for the sake of its deep scarlet flowers, the branches of the inflorescence and the pedicels stand out nearly horizontally from the stiff upright stem (see fig. 309 [1]). The pedicels are thickened just where they pass into the flowers and bent down so as to hold the flowers, when they are newly open, approximately at right angles to their stalks, which gives a curious appearance to the inflorescence as a whole. The flowers are protogynous, and, on the first day that they are open, the stigma can only be dusted with extraneous pollen from older flowers. The style is originally curved, so that the receptive tissue is held in front of the entrance to the floral interior where honey is abundantly secreted, and in this position it is inevitably brushed against by insects visiting the flower (fig. 309 [1], the right-hand flower). The next day the style straightens out, and the stigma is consequently moved away from the passage to the honey, whilst, on the other hand, the anthers open and place their pollen-coated faces exactly in the path of insects coming in search of honey (fig. 309 [1], the middle flower). On the third day the style becomes curved again and takes up the same position as it occupied on the first day. At the same time the pedicel undergoes further inflection and brings the tubular corolla nearer to the main axis of the inflorescence (fig. 309 [1], the left-hand flower). The result of these combined inflections is that the viscid stigma is brought right under the anthers at the time when they are shrivelling and catches a portion of

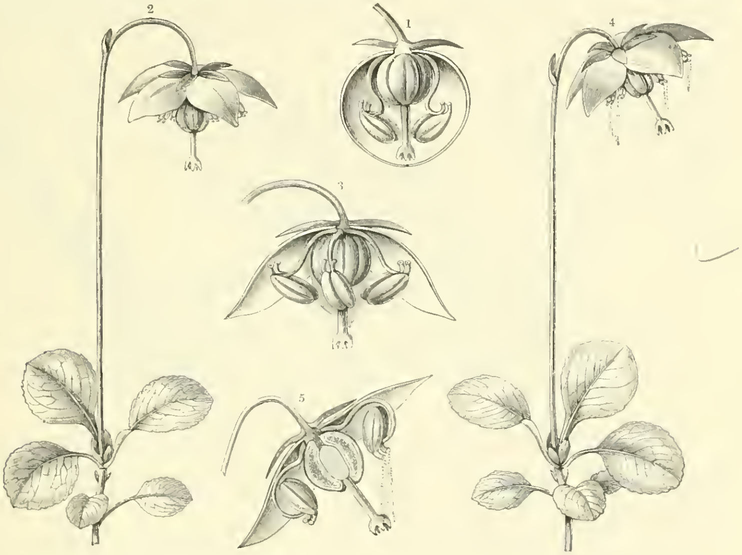


Fig. 308.—Autogamy caused by the combined inflections of pedicel and stamen-filaments: *Pyrola uniflora*

1 Longitudinal section through a bud about to open. 2 The whole plant with its flower in the first stage of development. 3 Flower in the first stage of development slightly magnified; the front petals are cut away. 4 The entire plant with its flower in the last stage of development. 5 Longitudinal section of a flower in the last stage of development; slightly magnified.

the crumbly pollen as it falls from them. Even if the pollen does not fall upon the stigma autogamy does not fail; for the corolla slips along the style as it drops, and is certain to touch both anthers and stigma, and to transfer to the latter the last grains of pollen adhering to the anthers (see fig. 309 ²).

Reference has often been made in former chapters to the splendid creeper named *Cobæa scandens*, one of the Polemoniaceæ native in tropical America, but capable of thriving luxuriantly in the gardens of Central and Southern Europe, where it is used for clothing espaliers, which it covers in the height of summer with deep-purple bell-shaped flowers (see fig. 310 ¹). The anthers are borne on long filaments with hairy bases, and are situated, at the commencement of the flowering-period, right in the mouth of the flower, where they are certain to be touched by insects which enter the flower to get the honey. The style is still short at this stage, and has its free extremity concealed under the anthers, whilst the three terminal branches of the style which bear the stigmatic tissue are closed tightly together (see fig. 310 ²). A little later anthers and stigmas change places; the filaments elongate and twist themselves into the form of corkscrews, and the anthers then rest lower than the three style-arms, which diverge and place themselves in a position to receive pollen brought by insects from younger flowers (see fig. 310 ³). If no insects make their appearance, and there is consequently no cross-fertilization, the pedicel undergoes inflection to the extent of about 45°, and the flower, hitherto nodding, becomes completely pendent. At the same time the style curves, and the coils of the stamen-filaments are drawn closer together. The result of all these movements is that the anthers are brought into contact with the stigmatic tissue, which is still receptive, and autogamy ensues (see fig. 310 ⁴).

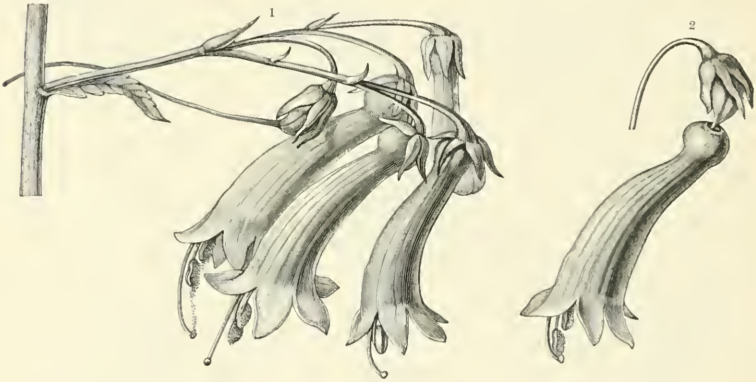


Fig. 309.—Autogamy ensuing in consequence of the inflection of the pedicel and the disarticulation of the corolla: *Phygelius capensis.*

¹ Portion of an inflorescence; the flowers borne by a horizontal branch of the inflorescence in the successive stages of development leading to autogamy (from right to left). ² A single flower at the moment of the detachment of the corolla and the rubbing of the anthers against the stigma.

Allium Chamæmoly (see fig. 311^{1}) is an example of the plants, in whose flowers autogamy is effected by concurrent movements of the pedicel and the style, the former undergoing inflection, whilst the latter is inclined in the direction of the spots where the pollen has been deposited. The small white flowers are lifted but a very little way above the ground; at first they face the sky, and are half hidden amongst the long green ribbon-shaped foliage-leaves. Nevertheless, they are assiduously sought out by small insects, the honey, which is secreted in little depressions on the surface of the ovary, being in great request. During the first stage of flowering cross-pollination alone is possible; the stigma is posted in the middle of the mouth of the flower, and its tissue is already receptive whilst the anthers are still closed and appressed to the walls of the perianth (see fig. 311^{2}). Later on all the filaments undergo inclination towards the middle of the flower; the anthers burst open, become covered all over with the pollen which issues from their loculi, and together form a yellow knob which occupies the centre of the entrance to the interior of the flower, and is brushed by all intruding insects. The stigma is at that stage hidden behind the anthers (see fig. 311^{3}), and is not touched by insects. If, for any reason whatever, insects do not visit a flower, autogamy takes place in the third stage of its development. The pedicel curves over downwards and presses the flower against the ground, and, as a consequence, the delicate white perianth-leaves and filiform stamens are displaced, and some of the pollen falls out of the anthers on to the lower perianth-leaves now resting upon the ground. The style undergoes slight lateral, *i.e.* in these circumstances downward, inclination and the final result of all these movements is that the stigma is brought into contact either with the

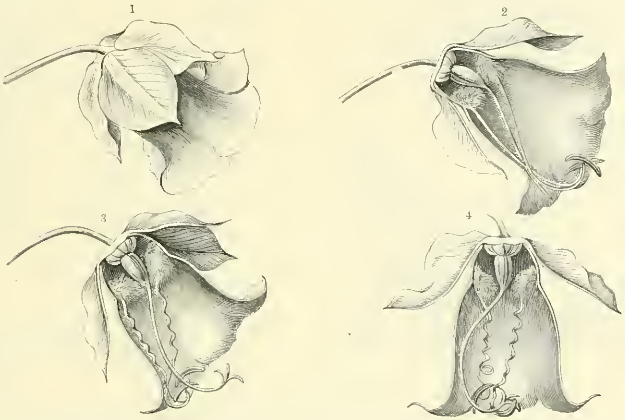


Fig. 310.—Autogamy resulting from an inflection of the pedicel accompanied by spiral torsion of the filaments: *Cobæa scandens.*

^{1} Side view of a newly opened flower. $^{2, 3, 4}$ Flowers in the three successive stages of their development which lead to autogamy. All the figs. somewhat reduced.

pollen lying on the lowest perianth-leaf or with that still sticking to one or other of the anthers (see fig. 311 ^{4}).

Of the plants in which autogamy is brought about by inflection of the pedicel combined with inflection or folding of the *petals,* two groups will be taken here as representing two different forms of the phenomenon. These groups consist of the Violaceæ of the *Melanium* tribe and the stemless Gentians. The manner in which the pollen is transferred to the stigma in Violets through the agency of insects has been already described on p. 280, and illustrated in figs. 279 $^{1, 2, 3}$ on p. 279. The pollen thus deposited by insects on the slightly-projecting flap of the capitate stigma is derived, of course, from other flowers, and the result of its transference is a crossing between the flowers either of one or of two species. Autogamy is in general scarcely possible in the Violet during the first part of the flowering-period. If pollen is shaken out of the cone of anthers on to the proboscis of an insect which is in the act of dusting the front surface of the stigmatic lobe with foreign pollen, this new supply may, perhaps, be rubbed off on to the back of the stigmatic lobe as

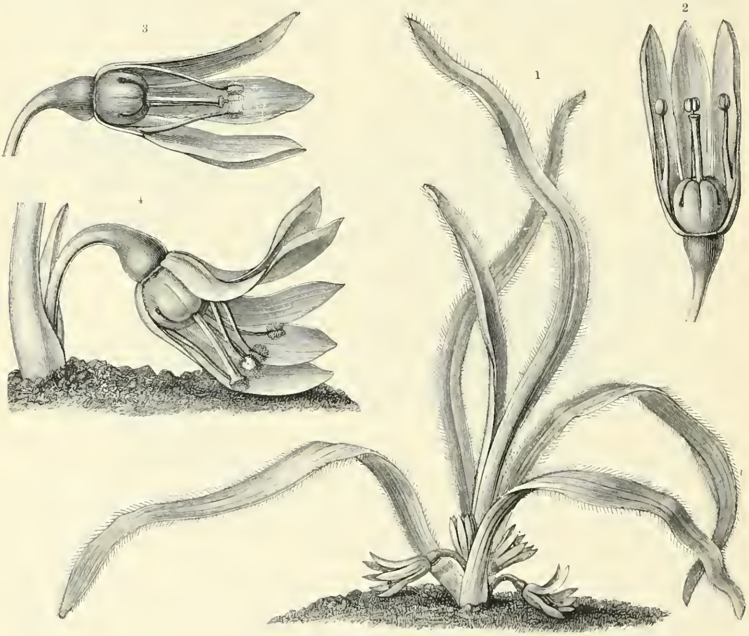


Fig. 311.—Autogamy resulting from inflection of the pedicel combined with inclination of the style to the place where the pollen has been deposited: *Allium Chamæmoly.*

^{1} Shows the aërial portions of the plant; nat. size. $^{2, 3, 4}$ Single flowers with the front perianth-leaves removed; slightly magnified. They are in the successive stages leading to autogamy.

the proboscis is withdrawn, but it does not even then come upon the receptive surface of the stigma. As regards the pollen which, though shaken out, is not carried away by the insect, but left lying underneath the cone of anthers in the trough of the spurred petal, it also does not reach the stigmatic tissue during the first stage of the flower's development, for the groove is still closed by the projecting lobe of the stigma. Towards the end of the flower's duration, however, the case is very different. The Violas of the *Melanium* tribe may be represented by the Field Pansy (*Viola arvensis*), it being the most widely-distributed species of the section. In these plants the cone of coherent anthers gradually breaks up of itself, and the pollen falls out, and fills the hinder part of the channel of the spurred petal. At the same time the lamina of this petal bends in such a manner that its trough is no longer closed by the stigmatic lobe, and the pollen is free to slip towards the mouth of the flower. The only condition now requisite is some change capable of setting the pollen in motion, and this is afforded by an inflection of the flower-stalk. Although the flower-stalk in the Field Pansy, Heart's-ease (*V. tricolor*), and other species of the *Melanium* tribe undergoes sharp inflection (see vol. i. p. 531) on clear nights, this movement has no influence in promoting autogamy at the time when the flower is in full bloom. At the last, however, it causes the mealy pollen to slip further and further down the groove in the lowest petal until it reaches the receptive stigmatic tissue.

There is a remarkable resemblance between this process and that observed to take place in those Gentians which are called by Descriptive Botanists "acaulescent" or stemless species (*Gentiana acaulis, G. angustifolia, G. Clusii,* see fig. 312). The flowers of these Gentians are of the type of "revolver-flowers" (*cf.* p. 250). The filaments are adnate to the lower part of the funnel-shaped corolla, and project in the form of five stout ridges towards the ovary, which appears as a column standing up in the middle of the flower; the ridges and the ovarian column, coming into contact with one another, divide the corolla into five tubular passages leading to the honey which is secreted abundantly at the bottom. The anthers are a little higher than half-way up the funnel of the corolla, and are connate into a tube which surrounds the style. Each anther dehisces extrorsely by two longitudinal slits, and immediately after the flower opens the anther-tube is covered all over with pollen. Above the tube is the stigma, which is composed of two notched and lacerated white lobes. The positions of the stigmas and anthers, respectively, ensure cross-pollination through the instrumentality of the humble-bees which fly from flower to flower. If, however, unfavourable weather prevails, and the bees stop away, the pollen gradually falls from the anthers as they shrivel, and is transferred to the stigmas in the same flower through the agency of the corolla and pedicel in the following manner. As long as the flower remains upright or ascends obliquely (see figs. 312 [1] and 312 [2]) the pollen falling from the shrinking anthers collects above the bases of the filaments, where they coalesce with the corolla, and when the corolla folds up for the night or to protect the pollen from rain, the pollen falls down between the folds, which, starting from close to the bases of the filaments, extend nearly to the mouth of the flower. These furrows constitute, in fact, the channels through which the pollen is afterwards conducted to the stigmas. The only movements needful for the attainment of this object are the inversion of the flower, and the placing of the stigma in such a position that its fringed edges may reach to the furrows in question. Both these conditions are complied with. The inversion of the flower is brought about by a considerable elongation of the pedicel, which is very short when the flower first opens, and by its semicircular inflection at the approach of night and in wet weather (see fig. 312 [2]). The introduction of the stigmatic margins into the furrows is due to the growth of the style, which carries the stigma up into the conical cavity formed near the apex of the flower when the corolla-limb folds up.

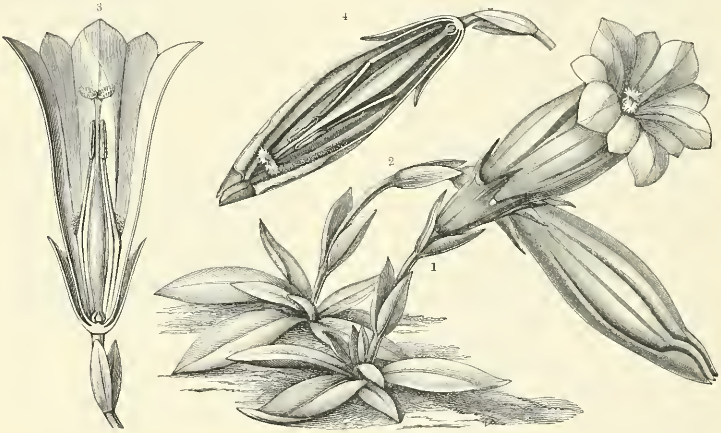


Fig. 312.—Autogamy resulting from inflection of the pedicel combined with the folding up of the corolla.

[1] *Gentiana Clusii* showing the flower as it is when opened for the first time. [2] The same plant with its flower in the last stage of development, the corolla closed and the pedicel elongated and curved downward in a semicircle. [3] Longitudinal section through a newly-opened flower. [4] Longitudinal section through a flower which has closed for the last time.

All the furrows of the corolla-tube open into this cavity, and converge into such proximity to the axis of the flower that contact with the edges of the stigmatic lobes, which occupy the middle of the conical cavity, is inevitable. If, under these conditions, the drooping flower is shaken by drops of rain falling upon it, or by gusts of wind, the pollen slips along the smooth furrow right down to the stigma, and is caught by its fringed margins (see fig. 312 [4]). It is worthy of note that *Gentiana acaulis*, *G. angustifolia*, and *G. Clusii*—the plants to which the above description applies—grow for the most part on grassy slopes, and on the ledges of precipitous rock-faces in the Alps; thousands of flowers of these species may be seen in situations of the kind with their heads drooping in wet weather so as to lie parallel to the slope of the ground, and fruits are invariably developed from these flowers, even after long-continued rain. On the other hand, flowers growing on flat meadows sometimes have no opportunity of becoming nutant. In them, as might be expected, autogamy fails, and if the weather is bad, and no humble-bees are about, cross-fertilization may also be prevented; therefore it is not unusual to find many ovaries unproductive in level places of the kind.

The Pasque-flowers, *Anemone Pulsatilla* and *A. vernalis*, may be taken as representatives of the cases in which autogamy is achieved by means of an inflection of the pedicels combined with an elongation of the sepals. The flowers of these plants have very short stalks and face the sky when they first open. They remain in that position for about forty-eight hours, opening in the daytime when it is fine, and closing at night and when it rains. No drooping of the flowers is to be perceived during the first two days, and indeed such a change would scarcely be possible, considering the shortness of the stalks. The flowers are markedly protogynous. The stamens are crowded together in large numbers, and their closed anthers, grouped in the middle of the flower, resemble the grains of a head of maize. Above the anthers rises a sheaf of styles bearing mature stigmas. Insects, especially hive- and humble-bees, are attracted at this stage of floral development by the honey which is secreted by small club-shaped nectaries interspersed amongst the sepals and stamens. On entering a flower they rub against the sheaf of stigmas, even if they have not actually used it as an alighting-place, and, in the event of their bodies having been besmeared with the pollen of older flowers, a cross with some plant which may be either of the same or of another species ensues. When two days have elapsed, the aspect of affairs is altogether changed. The peduncle has become considerably longer, and the flower nods slightly when darkness sets in; the inner stamens are no longer stiff but curve outwards, whilst those anthers which are nearest to the styles have undergone dehiscence and offer their pollen for dispersion. The sepals, which are concave towards the middle of the flower, have elongated somewhat to protect the pollen. Insects now come in quest of pollen as well as honey, and are certain to get dusted with a quantity of it which they may then transport to other flowers. When a flower closes in the evening, pollen from the anthers of the reflexed stamens is invariably affixed to the inner surface of the superincumbent sepals. At this stage, too, pollen is liable to be shaken out of the anthers of the longest stamens, and this falls, in the case of a nodding flower, on to the central stigmas of the fascicle of styles. Two days later, again, the condition of the flower is as follows:—The stalk is from ten to twenty times as long as it was, and the flower is nutant in the daytime as well as by night. The stamens have all relaxed from their rigidity; the filaments are curved outwards, and the anthers are open. The sepals have more than doubled their original length, and the pollen affixed to their inner surfaces has consequently been raised to the level of the stigmas. In addition, the form of the three inner sepals has changed; the concave inner face is now convex, and the external surface is concave. The result of these changes is that the stigmas at the periphery of the fascicle now receive their share from the elongated sepals, which are appressed to them and yield up to their receptive tissue the pollen sticking to their inner surfaces.

The processes which lead to autogamy in the Water Avens (*Geum rivale*), the Raspberry (*Rubus Idæus*) and some other Rosaceæ allied to these are even more complicated than those above described. Thus, for example, the flowers of *Geum rivale*, on the day that they open, face laterally and have their stalks horizontal; the filaments are short, and the anthers are all closed, while the stigmas which project in a tuft 2 mm. beyond the anthers are already mature. At this stage insects may occasion cross-fertilization, but autogamy is not yet possible. Subsequently, the filaments lengthen and the anthers of the longest stamens open and come into contact with some of the stigmas at the periphery of the bundle of styles. The pedicel is now curved and the flower nods; consequently, the pollen which falls from the anthers above, when they shrivel, is forthwith received by the outer stigmas of the fascicle of styles, that is to say, by those of the outer stigmas which appertain to the upper half of the flower. The pollen which falls from the anthers of the under half of the flower when they dry up, is caught, on the other hand, by the petals on that side of the flower, and is afterwards transferred, by means of an elongation of these petals, to the stigmas of the adjacent reflexed styles. A couple of days later the pedicel is curved into a semicircle, and the flower hangs down with its mouth towards the ground. By this time the anthers of the shorter stamens are open; the whole flower has become loosened, and the fascicle of styles resembles a sheaf of corn. All the styles, including those in the middle, become twisted and reflexed to the extent necessary to bring the stigmas underneath the most recently opened anthers, and when these anthers shrivel and the pollen is forced out, it falls upon the central stigmas, which hitherto have not been furnished with any. Thus, in this case we have (1) the inflection of the pedicels, (2) the elongation of the petals, (3) the elongation of the stamens, and (4) the inflection of the styles—all co-operating towards the same end, namely, that in the event of no insects visiting a flower all the stigmas may receive pollen from the anthers developed in the flower itself.

The foregoing descriptions, though extremely brief and cursory, give a general idea of the many kinds of contrivances whereby autogamy, as well as heterogamy, is promoted in hermaphrodite flowers. It is evident from them that any mechanism which leads to autogamy has full scope for its operation only if cross-pollination has not previously been effected. Again and again we have found that certain processes only take place in the event of a flower being unvisited by insects through whose agency cross-fertilization would have been brought about. In this connection we have also the remarkable phenomenon that many flowers adapted to cross-fertilization by insects do not open at all when there is no chance of their being visited by the agents in question. In the mountainous districts of the temperate zones it often happens that rainy weather sets in just at the time when the flowers are about to open, and that it lasts for weeks. Humble- and hive-bees, butterflies, and flies retire to their hiding-places, and for a considerable time cease to pay any visits to flowers. The growth of the plants is not, however, arrested during this period, and even in the flowers themselves development quietly progresses if the temperature be not too low. The stigmatic tissue becomes receptive; the anthers attain to maturity, dehisce and liberate their pollen notwithstanding that no ray of sunshine penetrates the clouds and that rain falls continuously. In such circumstances the mouth of the flower is not opened; autogamy takes place in the closed flower, and all the adjustments evolved with the object of ensuring cross-fertilization are ineffectual. This is the case, for instance, in the following:—*Alsine rubra, Anagallis phœnicea, Arabis cœrulea, Azalea procumbens, Calandrinia compressa, Centunculus minimus, Drosera longifolia, Gagea lutea, Gentiana campestris, G. glacialis, G. prostrata, Hypecoum pendulum, Hypericum humifusum, Lepidium sativum, Montia fontana, Oxalis corniculata, O. stricta, Polycarpon tetraphyllum, Portulaca oleracea, Sagina saxatilis, Silene noctiflora, Sisyrinchium anceps, Spergula arvensis, Stellera Passerina, Veronica alpina, V. bellidioides* and *V. Chamædrys*—plants which grow in widely different habitats, but which all have the common property that their flowers open for but a short period, if at all. In plants with long-lived flowers it is of not uncommon occurrence for autogamy to be accomplished during a spell of wet weather, and for the petals to open subsequently all the same, and so afford the possibility of the remains of the pollen being carried away by insects. This phenomenon has often been observed, for example, in *Rhododendron hirsutum*, the Bog-bean (*Menyanthes trifoliata*), and the Greater Dodder (*Cuscuta Europæa*).

There is also the case of such plants as *Alisma natans, Illecebrum verticillatum, Limosella aquatica, Peplis Portula* and *Subularia aquatica*, which live in pools or on the banks of ponds where the level of the water is variable. If the buds of these plants are submerged at the time when they are about to open, they do not unfold, and autogamy takes place in the closed flowers under water. It must be observed that the water does not penetrate into the air-filled interior of the flowers, so that we have here the curious phenomenon that the transference of pollen to the stigma, though accomplished under water, is yet a case of pollination in the medium of the air.

An allied phenomenon is exhibited by some of the Knotweeds (*Polygonum Hydropiper, P. minus*, and *P. mite*). Isolated plants of any of these species, in which all the flowering branches are exposed to the sunshine, and are both visible and accessible to insects, unfold all their flowers; but, if hundreds of one species are crowded close together, only a limited number of the flowers open their perianths. The flowers growing on the upright branches alone of such crowded plants unclose, and receive insects' visits, whilst those which grow on the under, procumbent branches, and are consequently concealed and not easily reached by insects, remain shut. Nevertheless autogamy is effected with obvious success in these also.

Plants of the kind just alluded to form a transition to those which normally produce two kinds of flowers, viz.: some which open and are adapted to cross-fertilization through insect-agency, and some which remain closed and exhibit autogamy with great regularity. The latter have received the name of *cleistogamic* (κλειστος=that can be closed, γάμος, marriage) flowers, and amongst them may be distinguished a series of very wonderful forms. A common characteristic of them all is the stunted development or complete abortion of petals which would otherwise attract insects by their scent, colour, or honey. The only function of the petals is that of an envelope under cover of which ovules and stigmas, anthers and pollen, attain maturity and are able to enter into combination with one another. In many cases there is no trace of a corolla to be seen; green sepals alone are developed into a floral envelope, and they are kept fast closed and cover the stamens and pistil in the form of a hollow cone. Thus, for instance, *Aremonia agrimonioides*, a plant growing abundantly in the forests of Carniola, has cleistogamous flowers about a millimetre in diameter, in which stamens and sepals spring from the edge of the excavated disc, whilst petals are entirely absent. In other cases, though petals exist, they remain small and of a greenish-white tint. Precisely those parts of the corolla which in open flowers are most conspicuous in form and coloration are here abortive. Thus, in the cleistogamous flowers of several species of Violet, the spurred petal, which in the open flower is the most striking, is scarcely recognizable; its lamina is oval in outline, and is rolled into a hollow cone covering the anthers and stigma. The anthers in most cleistogamous flowers are so situated that when the pollen is ripe and issues from the loculi it comes immediately into contact with the stigma. Sometimes, it is true, there is a tiny interval between the pollen adherent to the anther-lobes and the stigma, but in that case tubes are put forth by the pollen-cells in the direction of the stigma, and these tubes lay themselves upon the papillæ on the stigmatic surface and thence pursue their way to the ovules. In the cleistogamous flowers of the Henbit Dead-nettle (*Lamium amplexicaule*) it has even been observed that the anthers do not open, but that, nevertheless, pollen-tubes emerge from the pollen-cells, perforate the walls of the anther and grow in the direction of the stigma until they reach it. If a cleistogamous flower of this kind is examined after autogamy has been accomplished within it, one might at first sight think the anthers and stigmas were adnate to one another, so firm is the union of the pollen-tubes with the stigma.

As has been already said, all species of plants which produce cleistogamous flowers also develop other open ones. For the most part these latter possess very striking forms, scents, and colours, and are adapted to receive the visits of insects and to undergo cross-fertilization through their agency. It is interesting to note, however, that these open flowers possess none of the contrivances for effecting autogamy in the event of a dearth of insects. From these observations we are justified in supposing that we have here a sort of division of labour, inasmuch as the functions, usually discharged by one form of hermaphrodite flower alone, are here divided between two kinds of flower—both also hermaphrodite—viz., cross-fertilization is assigned to those that open, self-fertilization to those that remain closed.

Amongst Grasses, Rushes, Scirpuses, and other plants of the kind, which produce dust-like pollen in their hermaphrodite flowers, only a few species are known to possess cleistogamous flowers. The oldest established example is that of *Oryza* *clandestina*, a widely-distributed bog-grass allied to the Rice-plant. The panicles of this *Oryza* include chiefly flowers which remain closed and are adapted to autogamy; they develop only on their very highest branches a few flowers which open and may be cross-pollinated by the agency of the wind. On the other hand, the number of species possessing cleistogamous flowers to be found amongst plants with adhesive pollen, and liable to be crossed by insect agency, is very large. Numbers of tropical and sub-tropical Asclepiadaceæ, Malpighiaceæ, Papilionaceæ, and Orchidaceæ afford instructive examples of this phenomenon. The splendid colours of the open flowers in these plants attract insects, and if the flowers are visited cross-pollination is rendered inevitable by the various kinds of apparatus for pressing, sprinkling, or shooting the pollen upon the insects with which the flowers are furnished; but if in spite of allurements no insects arrive, the stigmas are not besmeared with pollen at all, and these great open flowers wither without forming fruit. It then comes to the turn of the cleistogamous flowers. They are developed in the axils of special leaves as small, greenish, bud-like structures, which are destitute of means for alluring insects, but are none the less sure on this account to produce ripe fruit and fertile seeds. There is, besides, in temperate zones, no lack of plants in which the same phenomenon may be observed. A host of Bell-flowers, Rock-roses, Balsams, Polygalaceæ, Oxalidaceæ, and Scrophulariaceæ (e.g. *Campanula, Specularia, Helianthemum, Impatiens, Polygala, Oxalis, Linaria*) and, in particular, the Violas of the *Nominium* and *Dischidium* sections, exhibit the same difference in the functions assigned to their two kinds of flowers. The beautiful *Viola mirabilis* has scented flowers stored with honey, which unfold great violet petals in the spring. If these blossoms are visited by hive- or humble-bees they are cross-fertilized; but many are not thus visited, and their fate is then to wither without effecting that process of autogamy which has been described (p. 387) as taking place in the species of Violet belonging to the *Melanium* section. In the summer, however, special branches of the same individual plant bring forth small green flower-buds which do not open, but nevertheless produce soon afterwards large ripe capsules full of seeds. This phenomenon, in apparent contradiction to the ordinary idea of the result of the flowering process, did not escape the attention of the Botanists of the eighteenth century, and they named this species of Violet, in which the majority of the large open blossoms fail to produce fruit whilst the closed bud-like flowers are invariably productive, *Viola mirabilis*, or the Wonderful Violet.

In *Viola mirabilis* and in all its allied species, called "caulescent" in the language of descriptive Botany, the cleistogamous flowers are developed on special shoots, and these shoots are either erect or else prostrate in long zigzags. This is also the case in several species of the Wood-sorrel genus (*Oxalis*) and in *Aremonia agrimonioides*. A few Papilionaceæ (e.g. *Vicia amphicarpa*) and Cruciferæ (e.g. *Cardamine chenopodiifolia*) are known too, whose cleistogamous flowers spring from underground runners or stalks, whilst the open flowers are borne upon aërial shoots. In several Violets of the kind called by descriptive Botanists "acaulescent", such as *Viola collina* and *V. sepincola*, the cleistogamous flowers develop likewise underground, their stalks springing from special shoots of the rootstock. In all these cases the two kinds of flowers are always borne on the same plant, though on different branch systems; there are, however, also instances, such as the Yellow Balsam (*Impatiens Noli-tangere*), where the open flowers are developed on different individuals from those which produce the closed ones. To be accurate we should say that the statement in each case expresses the general rule for the plants in question, for instances of transition are by no means uncommon. Thus, for example, individual plants of the Yellow Balsam do occur in which open flowers with large corollas, half-open flowers with stunted corollas, and small cleistogamous flowers stand side by side; and, again, on the zigzag runners of the Sand Violet (*Viola arenaria*) flowers with large expanded petals have often been seen growing in company with the cleistogamous flowers. The same remark applies as regards the time at which cleistogamous flowers make their appearance. In the majority of cases they are not developed until the open flowers have withered and disappeared, but in *Cardamine chenopodiifolia* it has been observed that the subterranean cleistogamous flowers are produced earlier than those which are borne on above-ground stems and unfold their petals to the air.

In former times it was asserted that plants exist which never bear any but cleistogamous flowers. Thus the Toad-rush (*Juncus bufonius*) was stated to produce cleistogamous flowers only. Later investigations have, however, established the fact that this plant possesses two kinds of flowers—viz. terminal flowers with three stamens which are cleistogamous, and lateral flowers with six stamens which open, like those of other Rushes, under the warmth of the noonday sun. It was also supposed that the African species of *Salvia*, to which the name of *Salvia cleistogama* was given, produced cleistogamous flowers only, but after repeated sowings plants have been obtained with flowers which opened. Anyone who has only seen the Yellow Balsam growing on the heaps of detritus brought down by the mountain-streams in the upland valleys of the Tyrol might think that this plant also was an instance of a species producing cleistogamous flowers only; for in those localities open flowers are not found on this species. But if seeds from these cleistogamous flowers are sown in good vegetable mould, in a partially shaded spot in a garden, a few individuals with large open yellow flowers spring up, as a general rule, even after a single sowing. There is a species of Violet named *Viola sepincola* which grows deep in the shade of the woods clothing the hills at the foot of the Solstein chain in the Innthal district. I saw it there for the first time about the middle of May, and it was then covered with an abundance of ripe fruit. In following years I looked for flowers of this plant early in the spring, as soon as the snow had melted, but found that not a single individual had developed open flowers with expanded petals on erect above-ground stalks. On the other hand, there were a number of cleistogamous flowers concealed under the fallen leaves and partially buried in the earth, so that it looked very much as if the species produced no other kind of blossom. But plants subsequently reared in a part of my garden which was exposed to the sun's rays during some hours of each day developed, in the next year but one after their being sown, in addition to cleistogamous flowers, beautiful scented blossoms of a violet colour which were borne on erect stalks and in due time unfolded their petals.

This result throws some light on the nature of the stimulus which causes the formation of the flowers in question. No open, aërial flowers were produced by *Viola sepincola* so long as it grew in the cool shade of a dense wood, but when transferred to open ground, accessible to sunlight, such flowers were developed. One can hardly err in ascribing to the sun's rays a very important influence in stimulating plants to the inception of flowering shoots, especially such as bear blossoms possessing bright-coloured petals. Indirectly, however, this advantage accrues to the plants in question that, living as they do in the deep shade, where no bees would, in any case, visit them, even if they had open flowers, they can confine their constructive energy to the inception and development of cleistogamous flowers and save themselves the trouble of producing open flowers adapted to cross-pollination (but useless in the place in question). If the spot where the Violet grows becomes exposed to the sunlight through the trees shading it being blown down or felled, humble- and hive-bees make their appearance in search of honey, and, buzzing from flower to flower, cross one with another. In such circumstances the open, sweet-scented Violet blossoms are in request, and the same plant-individual, which for years in the dark shade has developed none but cleistogamous flowers, is now stimulated by the sun's rays into producing flowers with expanded petals.

A similar instance is afforded by the Henbit Dead-nettle (*Lamium amplexicaule*), which grows on cultivated ground—in kitchen-gardens, vineyards, and amongst crops. This plant bears two kinds of flowers, viz. some with purple corollas 15 mm. in length, which keep the entrance leading to their honey wide open, and, secondly, cleistogamous flowers with abortive corollas and small green calices, which remain closed. As is the case with many other annual weeds, Dead-nettle plants which have germinated late in the season maintain their vitality through the winter and into the following spring, and accordingly they may be seen at all seasons flourishing, fresh and green, in situations such as are mentioned above. Flowers, too, are initiated and developed by them at all seasons of the year, but it is interesting to note that only in the warm summer, when flower-seeking insects are about, are the beautiful purple corollas of this plant to be seen; in the late autumn and early spring, when it is cool, and there are no flower-seeking insects, this Dead-nettle is able to do without the luxury of corollas, which are the means of alluring insects, and as a fact only cleistogamous flowers make their appearance at those seasons. It must not, of course, be imagined that the plant exercises an intelligent discretion of its own when it abandons the development of corollas. The connection between this effect and the aforesaid conditions is indirect, and we must conceive that the nature of the stimulus which results in the inception of flower-buds is different, when a plant is subject to the influence of the short days and low temperature of late autumn and early spring, from what it is under the conditions prevailing on warm summer days.

Amongst the contrivances mentioned in the last chapter as being adapted to bring about cross-fertilization at the commencement of a flower's period of bloom, was the production of heterostyled flowers (see pp. 302 and 312). It was pointed out (p. 316) that in heterostyled plants the very first, or last (as the case may be), of all the flowers of a particular species are, in consequence of the dichogamy which prevails, fated to be crossed with flowers of another species, or, in other words, to undergo hybridization, and that, according to experience, this crossing is often effective. Considering the results obtained in the cases of other plants with hermaphrodite flowers, one would expect to meet with some provision for the timely fulfilment of autogamy in heterostyled species as well, *i.e.* that in the event of no insects visiting a plant of the kind, the stigmas should at the proper moment be dusted with pollen from the anthers in the same flower. This expectation has been, in fact, confirmed; all the investigations directed to this question having resulted in showing that a process of autogamy takes place also in heterostyled flowers, but is always confined to one only of the forms which together constitute the species. In one section of the heterostyled species, including, for example, those which belong to the genera *Gentiana*, *Menyanthes*, and *Thesium*, the short-styled flowers are adapted to autogamy, whilst in others, such as the heterostyled species of *Mertensia* and *Pulmonaria*, autogamy takes place in the long-styled flowers. In *Primula longiflora* and *P. minima* it is the short-styled flowers which have their stigmas dusted with pollen from their own anthers, whilst in *Primula Auricula*, and *P. glutinosa* it is the long-styled flowers which thus accomplish self-fertilization. All these variations are exactly adjusted with reference to the other arrangements for promoting autogamy in the flowers in which they are exhibited.

One contrivance which deserves mention here is the disparity in the size and conspicuousness of the floral envelopes in the two forms of flowers of the same species. In *Primula longiflora* and *P. minima* the long-styled flowers, and in *Primula Auricula* and *P. glutinosa* the short-styled flowers have a larger and more striking limb to their corollas than the other forms in each case. It may be taken to be a general rule that the flowers adapted to cross-fertilization, in which no autogamy takes place, are larger than those in which the accomplishment of autogamy is assured. This phenomenon has been explained by the circumstance that flowers destined to be crossed with others require to be more plentifully equipped with the means of attracting insects than those which are certain to undergo fertilization even if no insects visit them.

The means whereby autogamy is achieved in species with heterostyled flowers are in the main the same as they are where the flowers are not heterostyled. In some cases the stamens, or the petals with pollen affixed to their surfaces, elongate sufficiently to enable the stigmas to come into contact with them: in others the same result is attained by an inclination or an inflection of filaments or style; in a third series the stigma is dragged through the ring of anthers when the corolla falls off, or the petals by opening and closing effect the transference of the pollen from the anthers to the stigma; and lastly, in some instances, the pedicels undergo elongation and inflection, which result in bringing the stigma underneath the anthers, so that when the latter shrivel their pollen must fall upon the receptive tissue. Of the host of observations relating to this matter, we can here only select a few to serve as examples, and the most suitable for our purpose will be the Primulas, to which reference has already been frequently made, viz. *Primula Auricula*, *P. glutinosa*, *P. longiflora*, and *P. minima*.

The corolla in the short-styled flowers of *Primula Auricula* has a comparatively large expanded limb, the surface of which is slightly concave; the five stamens are adnate to the contracted throat of the corolla, where the tube passes into the limb, and the anthers form, at that part of the flower, a ring through the middle of which insects must penetrate in order to enter the floral interior. The style is short, and the spherical stigma at the top of it stands at a level corresponding to only a third of the length of the corolla-tube. At the time when the dehiscence of the anthers takes place, the flowers are in a nodding or horizontal position. In these circumstances no pollen can reach the stigma, and, unless visited by insects, the flower remains unpollinated until it fades, nor does the fall of the corolla operate as a means of conveying pollen from its own anthers to the receptive tissue. It is quite different with the long-styled flowers of the species in question. The limb of the corolla is rather smaller, and is hollowed into the shape of a basin; the five stamens are adnate to the lowest third of the tube, and their anthers stand at the same height as does the stigma in a short-styled flower. The style is long, and the stigma may be seen in the middle of the flower's throat. In other respects there is no difference worth mentioning between the two forms. The stigmas of the long-styled flowers are liable to be dusted with pollen brought by insects from the anthers stationed in the throats of short-styled flowers. Whether this occurs or not, the receptive tissue under any circumstances gets covered with pollen when the corolla becomes detached and falls off, for the stigma is then dragged through the ring of anthers in the corolla-tube, and is certain to remove some of the pollen which still adheres in more or less abundance to them.

Altogether different is the process of autogamy as manifested in *Primula longiflora*. In this case the corolla of a long-styled flower has a shorter tube and larger limb than that of a short-styled flower. The anthers are situated in the throat just behind the mouth of the corolla-tube. The style is long and projects far beyond the throat, whilst the stigma is held considerably above, that is to say, in front of the ring of anthers. The flowers are either horizontal or else ascend obliquely, and neither of these positions admits of pollen being deposited by the anthers upon the stigma. As in this species the corolla does not drop but persists even when withered, no autogamy takes place in the long-styled flowers when the plant is growing wild. On the other hand, every insect which enters the flower must necessarily touch the stigma, stationed where it is in front of the passage, and cross-fertilization then ensues. The short-styled flowers have a longer tube and smaller limb to the corolla. Their anthers, unlike those of many other Primulas, are situated in the throat close beneath the corolla-limb in the same position as in the long-styled flowers; but the style does not project outside the throat, and its stigma rests only just above the tips of the anthers. Under these conditions cross-pollination is as likely to be brought about through insect-agency as it is in the case of the long-styled flowers; but in addition autogamy takes place towards the end of the period of bloom. The manner in which the latter is effected is as follows:—During the period of the flower's bloom the corolla-tube grows some millimetres in length until finally the ring of anthers, which are adnate to the throat of the corolla, is brought up to the same level as the stigma. The stigma then stands in the centre of the ring and receives an abundant supply of pollen from the adjacent anthers.

In *Primula minima* (see figs. 288[1] and 288[2], p. 302) the heterostyled flowers are erect and maintain this position unaltered till the corolla withers. The limb of the corolla in the long-styled form (see fig. 288[1]) is larger than it is in the short-styled form. The anthers in the long-styled flower are inserted on the lower part of the tube; the style projects above the ring of anthers and the stigma rests somewhere in the uppermost third of the tube. On entering a flower an insect would first come against the stigma, and would then probably dust it with foreign pollen. Autogamy scarcely ever takes place. In the wild state of the plant the corolla withers without falling off; only in rare instances does it happen that the corolla becomes detached from the receptacle, and is carried away by the wind. On such an occasion the stigma might touch the ring of anthers and get covered with pollen. Self-fertilization is, on the other hand, all the more carefully ensured in the short-styled flowers. Here the anthers are attached to the highest third of the corolla-tube, and the stigma capping the short style rests below the ring of anthers. When the flower's period of bloom is nearly at an end both the corolla-tube and the anthers begin to wither and contract, with the result that the pollen falls from the anthers down the tube, and is caught upon the stigma.

Thus, autogamy is effected in the long-styled flowers of *Primula Auricula* and *P. glutinosa* by the stigma being dragged through the ring of anthers as the corolla falls off, in the short-styled flowers of *Primula longiflora* by the elongation of the corolla-tube and elevation of the anthers to the level of the stigma, and in the short-styled flowers of *Primula minima* by the anthers shrivelling and letting their pollen fall. The fact of the occurrence amongst Primulas alone of three kinds of contrivance for promoting autogamy gives us some idea of the immense variety which prevails in this respect amongst heterostyled plants in general. The impossibility of entering here into the further details of this subject is the less to be regretted, seeing that to a great extent such an account would involve a repetition of facts which have already been stated.

The number of species possessing heterostyled flowers is far larger than was formerly supposed. The list of such species known at the present day includes members of the following families: Boraginaceæ, Caprifoliaceæ, Caryophyllaceæ, Colchicaceæ, Crassulaceæ, Ericaceæ, Gentianaceæ, Globulariaceæ, Iridaceæ, Linaceæ, Lythraceæ, Onagraceæ, Oxalidaceæ, Papaveraceæ, Plantaginaceæ, Plumbaginaceæ, Polygonaceæ, Primulaceæ, Rubiaceæ, Santalaceæ, Solanaceæ, and Valerianaceæ, and it is probable that more thorough investigation will result in the addition of many more instances, especially amongst tropical plants. In most cases the species of one genus produce only two forms of flowers; but there are also genera—such as *Linum* and *Oxalis*—in which some of the species develop long-, mid-, and short-styled flowers, others long- and short-styled forms, and others again none but flowers with styles of equal length. The determination of the point as to whether heterostylism exists or not in a particular case is, in many species, attended with some difficulty, owing to the stamen-filaments increasing in length during the period of the flower's bloom in both the long-styled and the short-styled flowers—a circumstance which greatly complicates the relations subsisting between the two forms in respect of the lengths of their different parts. There is also some danger of mistaking for heterostyled species a class of forms which do not in reality come under that category. In the species alluded to, a proportion of the individual plants produce apparently hermaphrodite flowers, with ovaries, styles, and stigmas which can be clearly identified as such, but which nevertheless are not capable of undergoing fertilization.

The results of the investigations into the subject of autogamy recorded in this chapter may be summed up as follows. In plants whose flowers are hermaphrodite, but neither cleistogamous nor heterostyled, both cross- and self-fertilization occur in one and the same flower at different epochs; in plants with cleistogamous flowers a division of labour is established between two kinds of hermaphrodite flowers, of which the one form opens and is adapted to heterogamy, whilst the other remains closed and can only result in autogamy; and, lastly, in heterostyled plants, each species includes two or three different forms of individual, varying in respect of the structure of the flowers, which in the one case aim at cross-fertilization, and in another especially at autogamy.

In view of the detailed consideration which the methods for promoting autogamy in various plants has received in the foregoing pages, it may not be without interest to allude here briefly to the relative prevalence of this mode of pollination in certain Floras. During the passage of the present edition of this work through the press, a notable addition to our knowledge of Floral Biology has been made by E. Loew (*Blütenbiologische Floristik*), in the form of a treatise wherein are summarized the vast number of observations upon flowers and their relations to insects, &c., so far as the Floras of Europe and Greenland are concerned, that have been published in one place and another during the last ten years. This tabulating of observations has enabled the author to make many interesting comparisons between the Floras of various regions, and, supported by statistics, to exhibit the relative prevalence of types adapted to this or that method of pollination. Though many of the results do but confirm views already the common property of Biologists, they have an altogether special value from the manner in which they have been obtained.

As regards autogamy, it appears from statistics that it shows an increase in high Alpine forms as compared with plants from a lower level. The accompanying table, taken from Loew, contrasts alpine and sub-alpine plants in regard to the relative prevalence of autogamy:—

(I.) Of 130 entomophilous plants in *sub-alpine* regions—
35 species = 26·9% are rarely or never autogamous.
86 species = 66·1% are autogamous as well as heterogamous.
9 species = 6·9% are invariably or usually autogamous.
99·9%

(II.) Of 133 entomophilous plants in *high alpine* regions—
35 species = 26·3% are rarely or never autogamous.
78 species = 58·6% are autogamous as well as heterogamous.
20 species = 15·0% are invariably or usually autogamous.
99·9%

Thus we see that 20 high alpine species show pronounced autogamy as compared with 9 sub-alpine forms.

In the mountain Flora of Scandinavia the prevalence of autogamy is even more marked.

(III.) Of 74 species from the Dovrefjeld—
12 species = 16·2% are rarely or never autogamous.
40 species = 54·0% are autogamous as well as heterogamous.
22 species = 29·7% are usually autogamous.
99·9%

As compared with the high alpine plants (table II.) we note a diminution of $10^{\circ}/_{\circ}$ in those which are always heterogamous, and an increase in those usually autogamous of some $15^{\circ}/_{\circ}$.

In plants whose distribution is restricted to the Arctic regions, the number of autogamous plants is in the majority.

(IV.) Of 45 species of purely Arctic plants—
0 species = 0·0% are almost exclusively heterogamous.
14 species = 31·1% are autogamous as well as heterogamous.
26 species = 57·8% are usually autogamous.
5 species = 11·1% are doubtful.
100%

Precisely what factors in their environment have led to this increased prevalence of autogamy in high alpine and far northern species is at present not certainly determined. A lack or comparative rarity of insect-visitors on the one hand, or unfavourable climatic conditions on the other, might either of them well lead to such a condition. Regarding the alleged paucity of insects in the Alps, one so well qualified to speak as Hermann Müller says[1]:—"I have not been able to convince myself that alpine flowers are, on the whole, less frequently visited and crossed by insects than are those of the plain". Nor does Loew, with the statistics before him, dissent from Müller's opinion. So also with regard to the northern types, concerning which the view is widely spread that their preponderating autogamy is connected with the paucity of insects. Loew is of the opinion that the insects there are adequate for the work they have to do, *i.e.* are sufficiently numerous for the maintenance of the species of plants which depend upon their visits.

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[1] *Alpenblumen*, p. 547.

Putting aside the visits, and proceeding to consider the climatic conditions, we are on much surer ground. Both on the mountains and in the far north the period of vegetation is a short one, and the shortness of the summer, combined with the broken character of the weather, which is common to the Alps and Arctic regions during that period, can hardly fail to promote autogamy amongst the plants growing in those regions. Such as have flowers that can pollinate themselves spontaneously will be more sure of ripening their seeds before the brief summer ends than will such the flowers of which must wait for insects. In the foregoing pages several instances have been described in which autogamy is promoted by the closing of the flowers. By these movements the pollen is mechanically transferred to the stigmas. It may well be that by the considerable increase which must accrue in these closing movements, owing to the frequency of unfavourable weather in alpine and arctic regions, a further condition favouring autogamy is obtained.

FERTILIZATION AND FORMATION OF FRUIT IN PHANEROGAMS.

Pollination, or the dusting of the stigma with pollen, is only the prelude to the phenomenon known as *Fertilization.* It is important to distinguish clearly between these two events, especially as the term "fertilization" is frequently used by authors when they really mean "pollination"—indeed, this substitution is almost inevitable in many cases, the custom being what it is. Fertilization can only occur in Phanerogams after previous pollination, though pollination does not invariably connote a subsequent fertilization. Thus, cases are known in which flowers, pollinated by insects at the proper time, do not produce fruit, and others in which the pollen of the same flower falls upon the stigmas with a like failure of result. In other words, both cross-pollination and autogamy may be without result.

It must be explained, to prevent misunderstanding, that the older accounts of this lack of result attending pollination should be received with caution. Formerly, judgment was passed rather hastily as to the results of pollination in hermaphrodite flowers, as it seemed obvious that the sexual elements must, unavoidably, come together. If no production of fruit took place in a really hermaphrodite flower, it was assumed that pollination was without result, and no precautions were taken to demonstrate that pollination had actually occurred. Thus it happened that certain plants were regarded as sterile, although this sterility had only been observed upon isolated specimens growing in gardens. In many cases the flowers of the plants in question were strongly protogynous, *i.e.* at the time when the stigmas should have been pollinated there was no pollen, there being no plants growing near with flowers in a more advanced stage. Similarly, such flowers cannot be autogamous, as the two sets of organs are never at maturity simultaneously. They are marked out for cross-pollination. When for any reason this does not take place, fertilization and fruiting obviously cannot occur. It is instances of this kind that are adduced by the older botanical writers to prove that the hermaphrodite flowers of certain species are infertile.

Plants have also been regarded as sterile from the fact that the particular insects necessary for the transfer of their pollen were absent from the locality in which the observations were made. Thus, *Paederota Ageria*, a plant not infrequently found in rocky crannies in the Southern Alps, and cultivated in large quantity in the Innsbruck Botanic Garden, was always found to be sterile in the last-mentioned locality, although it flowered profusely. The flowers of the plant require insects to pollinate them, as the relations of the parts are such that autogamy cannot occur. Since the particular insects which visit it in its own habitat are absent from the Botanic Garden, the plant is infertile from lack of pollination. In its own home in the Southern Tyrol and Krain, where these insects are present, it ripens an abundance of fruits. The same is the case with several introduced plants which have become partially wild. The Sweet Flag (*Acorus Calamus*), truly indigenous to Eastern Asia, has spadices of densely-crowded, hermaphrodite flowers. The individual flowers are strongly protogynous, and when the anthers open, the stigmas of the same flower are already faded. Autogamy is consequently excluded. The opening of the flowers is from below upwards, and when the anthers of the lowest flowers are discharging their pollen the stigmas of the uppermost flowers are still capable of pollination. Could the pollen pass from the lower to the upper flowers, geitonogamy would take place, but this is only possible through the agency of insects, as the pollen is adhesive. In Europe, where the plant is not originally indigenous, this never happens, as the insects which visit it are absent; consequently, with us, *Acorus* is always sterile. But further east, where it is indigenous, its flowers are pollinated by insects, and it produces its fruit in spikes of red berries. The Day Lily (*Hemerocallis fulva*) has ephemeral flowers which open in the morning in summer-time between 6 and 7 o'clock, and close between 8 and 9 in the evening. Its flowers are protogynous for a very short time. For half an hour before the opening of the flower the mature stigma projects from the tip of the perianth. Simultaneously with the folding back of the perianth, the anthers liberate their adhesive pollen. The style being longer than the stamens, its stigma is not automatically pollinated. For pollination insect visits are necessary. Honey is secreted at the base of the tube of the perianth, which is 2 cm. long. The entrance to this honey is so narrow that only a very delicate proboscis can gain access. Beetles, flies, bees, and other short-tongued insects cannot get it, nor would they be of any use for pollination if they could. The whole flower seems adapted for the visits of some large butterfly with a long, thin proboscis, but curiously enough the flowers of *Hemerocallis fulva* are never visited by butterflies in Europe. As autogamy is excluded, the flowers remain unpollinated, and are sterile. Neither in gardens, where it is much cultivated, nor in its semi-wild state does the Day Lily ever fruit with us. It is more than probable that *Hemerocallis* is visited, in Northern Asia and Japan, where it is truly indigenous, by some butterfly absent from Europe.

It has been already mentioned (p. 156) that the flowers of the American Yuccas are pollinated by small moths, unknown in Europe, and that these flowers set no fruit with us. Also, that several species of Catchfly, indigenous to the Southern and Eastern Alps, though robbed of their honey by humble-bees, are but seldom pollinated and fruitful (p. 239).

Lastly, many cultivated plants, depending on insects for fertilization, flower in gardens earlier or later than in their wild surroundings. In nature, their period of flowering coincides with the time of flying of certain insects; in gardens—even when the insects in question occur—the flowers may be too early or too late for the insect season. From what has been said above, it will appear that sterility in many cases is only apparent, and is due merely to the lack of the normal and necessary conditions for bringing about pollination.

In other cases it may happen that although the stigmas are pollinated, the pollen cells are abortive and incapable of producing pollen-tubes. This condition of the pollen obtains most frequently in gardens amongst plants on rich, well-manured soil, artificially-produced hybrids, and plants whose stamens are partly converted into petals. At the same time it must not be supposed that by any means all plants which show a "doubling" produce bad pollen; for instance, many double Roses produce pollen which is used by gardeners for artificial pollination with good results. Still, in the majority of such plants abortive pollen is the rule, pollen which is non-effective on the stigma.

In nature, especially in places where many plants flower at the same time, as on the borders of a wood, in meadows and heaths, it is unavoidable that the pollen of various species should be deposited on one and the same stigma. Insects certainly show a preference for a single species for considerable periods, particularly when this species is flowering in quantity on a confined space; still, anyone who closely observes insects visiting flowers can easily convince himself that the flowers visited are changed from time to time. A bee which has just dusted itself with pollen in the flower of a Winter Aconite (*Eranthis*) will fly across to visit a bush of *Salix daphnoides*, and as it passes a plant of *Daphne Mezereum* it will suck its honey; a moment later it will swoop down to the flowers of *Crocus vernus* in the meadow near by, and then fly on to the Sweet Violet (*Viola odorata*). On the stigma of the last-mentioned plant will be found the pollen of all or several of the just-visited flowers, on the Crocus that of the Willow, and so on. The case is similar with wind-pollinated flowers. I have found the pollen of the Spruce Fir (*Abies excelsa*) and of Dog's Mercury (*Mercurialis perennis*), both brought by the wind on to the stigmas of the Herb Paris (*Paris quadrifolia*); and on another occasion the stigmas of *Gagea lutea* were so thickly dusted with the pollen of *Alnus viridis* that there would have been no room for any pollen more.

That the pollen of the Willow will fertilize the Crocus, that of Dog's Mercury the Herb Paris, or that of the Alder the Gagea is *a priori* improbable. Only such changes take place in the pollen as always occur when it is placed on a moist substratum; all further stages in its development are arrested. The commencing pollen-tubes, sometimes found, though in some cases they penetrate the tissues of the stigma, do not fertilize the ovules. It is another question whether or no this "foreign" pollen is entirely without effect, whether it does not possibly influence the stigmatic tissue so that less foreign pollen, arriving later on the same stigma and developing pollen-tubes, is affected. But this subject can only be dealt with later on; here it suffices to state that all pollen falling on a stigma is not necessarily suitable, and that the stigma has, in a manner of speaking, to make a selection.

It is very difficult to say what conditions come into play in this choice of pollen. Experimental inquiry into this matter has not been wanting, but its results tell us little as to the fundamental processes at work. By it we ascertain little more than whether this or that artificial pollination leads to a production of seeds or not. Thus in one case no seed will be formed, in another a few, and in a third case an abundant crop. The sources of error in this class of experiment are considerable, nor do the results by any means always harmonize. Thus, in experiments of my own as to the fertility of certain Catchflies when pollinated from allied forms, no result would be obtained in one year, whilst in the following year their repetition led to the production of a certain number of seeds. Other observers have had the same experience; and it would seem that whatever care be exercised, absolute reliance cannot be placed on the result—especially where it is a negative one. Caution must be used, therefore, in generalizing from such experiments, especially in cases where their number is limited. In the main, the general results are very instructive, and must not remain unnoticed here in so far as they relate to the connection between fertilization and the origin of new species.

These results may be shortly summarized as follows. When the pollen of one species is placed on the stigma of another species, pollen-tubes capable of fertilizing the ovules are developed only when the two species belong to the same genus or to the same natural family of plants. Families and genera are conceptions devised by Botanists, and although their limitations are to some extent arbitrary or dependent on the personal equation of individual observers, in the main there is little difference of opinion as to these limitations in the case, at any rate, of families. How far new discoveries may lead to a revision of their present limits must remain undecided, but, of families as at present laid down, we may say that crossings of pollen between species of two different families (orders) is without result, whilst between species of two different genera very rarely is seed produced.

The crossing of species of the same genus results, in most cases, in fertilization, and eventually in the production of hybrids. It is certainly remarkable, in this connection, that external similarity between the two species crossed has little bearing on the result or absence of result. One of the commonest of naturally-produced hybrids is one which owes its origin to the union of *Primula glutinosa* with *Primula minima*, two species very dissimilar in the form of their foliage and flowers. On the other hand, hybrids of the very similar Cowslip and Bardfield Oxlip (*Primula officinalis* [*veris*] and *Primula elatior*) are but rarely met with in nature, whilst artificial pollinations between them only occasionally lead to any result.

If ripe pollen from the male flowers of a plant be placed on the mature stigmas of female flowers of the same species, the result may be regarded as certain. This holds good equally for monœcious and diœcious plants, and for such also as have apparently hermaphrodite flowers in which one or other set of sexual organs is more or less abortive, so that the flowers in question are to all intents and purposes unisexual.

It has been shown that for plants with true, non-heterostyled, hermaphrodite flowers, a transfer of ripe pollen from the anthers of one flower to the mature stigma of another, belonging to the same species, constantly leads to fertilization. In those cases only in which the stamens are of unequal lengths is pollination attended with unequal results, according as the pollen has been taken from the longer or shorter stamens.

The behaviour of plants with hermaphrodite heterostyled flowers is peculiar. Pollen from the anthers of a short-styled flower applied to the stigma of a long-styled flower, or from a long-styled flower applied to the stigma of a short-styled flower, gives the best result. The other possible combinations, *i.e.* pollen from long-styled or short-styled flowers applied to the stigmas of the same class of flower give indifferent results, and frequently none at all. Experiments have shown in the case of the Loosestrife (*Lythrum Salicaria*), which, as we have seen (p. 303), possesses long-, mid-, and short-styled flowers, that crossings between stamens and styles of the *same* length ("legitimate unions") are fruitful, whilst all other crossings ("illegitimate unions") are either quite sterile or followed by only a sparing production of seed.

It has been demonstrated that the pollen-cells of heterostyled flowers vary both in size and colour according to the length of stamen (or height of anther or corolla) producing them. Thus, in the Loosestrife, the dry pollen-cells of the long stamens are green, and 30–38 μ long and 20–26 μ broad; those of stamens of the middle length are yellow and 23–26 μ long and 13–16 μ broad; those of the short stamens are also yellow, but 20–25 μ long and 11–13 μ broad ($\mu = \frac{1}{1000}$ millimetre). In the Cowslip (*Primula officinalis* [= *veris*]) the pollen-cells, produced by anthers at the mouth of the corolla-tube (and destined for a long style), have a diameter of 30 μ, those arising from anthers low down the tube (and destined for a short style), a diameter of only 20 μ. The explanation offered by Delpino of this difference in size—that, other things being equal, pollen-tubes which have to traverse a greater distance to reach the ovules require a more ample supply of reserve-materials than those which have less far to penetrate—sounds plausible, but the problem is probably a rather more complex one than appears at first sight. As a general result of experiments upon heterostyled plants we may say that the most copious production of good seed results from a pollination of stigmas with pollen from stamens of similar height.

As to the result of *autogamy* (self-pollination) in ordinary hermaphrodite flowers, it would appear, in all cases where the stamens are of unequal heights, that the pollen has a dissimilar effect according as it comes from a longer or shorter stamen. If pollen, which *would not unaided reach the stigma* of the same flower, be artificially transferred to that stigma, the product is usually very small. If, however, *pollen which would ultimately reach the stigma* of the same flower be artificially transferred thither a good crop of seed results. Artificially produced autogamy in hermaphrodite flowers, in which the stamens are all of one length, is generally productive, nor does it appear to matter whether the pollen used for pollination be taken from the first stamen to open or the last. The number of species in which artificial autogamy is unfruitful is extremely small. *Crambe tataria, Draba repens, Lilium bulbiferum, Lysimachia nummularia,* and a few Orchids and Papilionaceæ may serve as examples, though even in these cases it is quite possible that some source of error, such as was mentioned at the commencement of this chapter, has been overlooked.

We may now proceed to discuss what is known as the *prepotency of foreign pollen over own pollen.* The term "foreign" is used of pollen upon a stigma which has been brought from another flower of the same or of some other species; "own" pollen, on the other hand, is applied to such as has originated in one of the anthers of the *same* flower. These terms are employed for the sake of brevity. If one examines a flower of *Corydalis* early in the morning of the day on which that flower will become accessible to insects, one finds that the anthers have already dehisced, and that the stigma is covered with own pollen. The stigma, lying between the two spoon-shaped petals, is regularly embedded in pollen. But as yet the stigma is immature and unreceptive, so that the absence of any interaction between pollen and stigma at this stage is intelligible. When insects come in due course, a portion of this pollen will be removed (*cf.* p. 266). Should the insects have visited *Corydalis*-flowers previously, they will leave some of the foreign pollen with which they are dusted upon the stigma at the moment when they remove some of the own pollen. The stigma is now in contact with both own and foreign pollen, nor will additional insect-visits materially alter this state of affairs. In due time the stigma becomes receptive and exerts a selective action upon the pollen. Though the process, as it takes place here, cannot be followed step by step, still we are justified in assuming, on the results of many experiments of artificial pollination, that the foreign pollen receives the preference. It has been shown for *Corydalis cava* that the flowers are absolutely barren to their own pollen, only slightly fertile to pollen from another flower on the same plant, and only thoroughly fertile when impregnated with pollen from a different plant. For other species, however, e.g. *Corydalis capnoides, fabacea,* and *ochroleuca,* it has been shown that the plants are fertile to their own pollen, so that if no insect-visitors come, the flowers do not remain sterile.

These results show how fallacious it would be to make the condition obtaining in *Corydalis cava* the basis of any far-reaching generalization, such as that autogamy is prevented, and without result. In point of fact, autogamy is highly productive in most species of *Corydalis,* and occurs, in such plants as are unvisited by insects, in the closed flower in a manner recalling that form of autogamy known as cleistogamy (*cf.* p. 391). That foreign pollen is prepotent in *Corydalis capnoides, fabacea, ochroleuca,* &c., when both foreign and own pollen are present on the stigma together, is neither asserted nor denied, though, in view of all the circumstances, it seems probable.

In agreement with *Corydalis* stand numerous species of *Fumaria*, and a great number of Papilionaceæ, especially those whose flowers possess a piston-apparatus (*cf.* p. 260). *Pisum* and *Ervum*, *Lotus* and *Melilotus*, the various species of *Trifolium*, almost all of them, when unvisited by insects, ripen seed, only a few species here and there being infertile when dependent upon their own resources. Thus we may say that when the stigma has to choose between own and foreign pollen, the latter probably gets the preference, though, when own pollen alone is present, it is adequate for fertility.

A similar condition obtains amongst the Scabiouses (*Scabiosa*) also. Their flowers are hermaphrodite and protandrous, and united into heads. At the time when the anthers dehisce, the pollen remains hanging to the stigmas, although these are not as yet actually receptive. For the time being, this pollen is without effect. By the visits of insects a portion of this pollen is removed and replaced by foreign pollen, which is ultimately, on the maturing of the stigmas, probably preferred to the own pollen. In the absence of insects, however, the flowers are undoubtedly fertile to their own pollen.

Likewise, in many Labiates (e.g. *Leonurus heterophyllus*) and Scrophulariaceæ (e.g. *Linaria littoralis* and *minor*), has essentially the same state of affairs been shown to exist. One more instance only need be described, that of a Catchfly (*Silene noctiflora*). This plant opens its flowers at about seven in the evening. If, however, the flowers be opened artificially a little earlier, at about six p.m., it is found that all the anthers have already dehisced, and that the delicate stigmatic papillæ are already dusted with the pollen from the five short stamens. Thus, already in the bud, autogamy has taken place in a manner not unlike cleistogamy. As the flowers open in spite of this, it can only be on the chance of crepuscular or nocturnal moths visiting them and bringing foreign pollen. The flowers of this Catchfly are not very eagerly sought after by insects, still now and again a *Plusia* or other owlet moth may be seen flitting from flower to flower, sucking honey and bringing and taking pollen. Thus, again, a selection of pollen by the stigma probably occurs with preference for the foreign; otherwise, why need these flowers open at all since the stigmas are already coated in the bud with own pollen? In the absence of insects the own pollen will be potent and lead to seed-production. In wet, cold weather also, when the flowers do not open at all, the ovules ripen into seeds, no doubt impregnated by their own pollen. In all the cases enumerated the behaviour is essentially the same, in the early stages of flowering the opportunity is given for cross-pollination by insects, but, wanting this, autogamy or self-pollination ensues.

We may now pass on to speak of the *germination of the pollen-grain* upon the stigma and of the development of the pollen-tube. The pollen is at this stage influenced by the receptive stigma. There would appear to be a taking up of fluid matter by the grain, though its exact nature has not been accurately determined. Since, however, pollen-grains germinate readily in a 3-per-cent sugar-solution, it is extremely probable that sugar is an important component of this stigmatic fluid.

The first demonstrable stage in the production of the pollen-tube is the pushing out of the delicate inner coat of the grain in the form of a tube through the thin places in the extine. The structure and distribution of these thin spots has been already described (p. 102); it need only be added that a tube may be pushed out at each or any of them. When pollen is artificially cultivated in a prepared sugar-solution several tubes arise simultaneously from different spots, but, in nature, on the stigma, the production of a single tube is the rule. The tube which contains the whole of the contents of the pollen-grain (spermatoplasm) forsakes the extine, which remains behind as a dead shell. Very soon after its appearance through one of these holes in the extine, the pollen-tube comes to have a considerable diameter, often approaching that of the grain in size. The tube now elongates, growing always at the expense of the stigma. Its mode of growth is similar to that of a fungal hypha, and its relation to the stigmatic tissues resembles that of the hypha of a parasitic fungus to its host. Like the parasite, it is able to penetrate the subjacent tissue and to make its way through it for long distances.

This penetration by the pollen-tube is certainly amongst the most remarkable properties of flowering plants. The object of these wanderings is to reach and fertilize the ovules contained—in Angiosperms—in the closed chamber of the ovary. Whether the stigma be sessile upon the ovary or situated upon a style, the distance to be traversed is considerable, and, in a very large number of cases, the way leads through closed tissues. As the pollen-tubes travel as a rule by definite rows of cells or tracks, we may assume that these latter are in some way specialized for their conduction; still it is very puzzling to understand exactly in what manner these cells become thus qualified. In all likelihood the pollen-tubes are attracted by certain substances secreted by the tissues, which they have to traverse in order to reach the ovules. Of these sugar seems to be the most important, and by a continuous secretion of this (and possibly other substances), the tubes are led on to the ovules. Casual allusion has already been made to the fact that the motile spermatozoids of Cryptogams swim through the water to the archegonia (amphigonia) in response to a somewhat similar stimulus (p. 68).

Investigations into the course followed by the pollen-tubes in passing from the stigma to the ovules show that it varies in different cases. Simplest, and perhaps typical of what was formerly supposed to be the route universally followed, is the case of the Martagon Lily (*Lilium Martagon*, *cf.* fig. 313 [1]). If the columnar style of this plant be cut longitudinally one sees that it is penetrated by a canal which narrows below towards the ovary, but widens out into a funnel at the stigma, where it opens by a tri-radiate slit. The lips of this aperture bear numerous papillæ; to these the pollen-grains become attached and here commence to form their tubes. The tips of the pollen-tubes curve down into the funnel and grow along the cells which line the style-canal (fig. 313 [1]). Passing down this canal, which is at this time more or less mucilaginous, the pollen-tubes are led ultimately to the cavity of the ovary in which are contained the ovules.

Very different is the mode of travelling of the tubes in Grasses, of which *Avena elatior* (fig. 313 [2]) may be taken as type. Upon the spherical ovary of this plant two delicate feathery stigmas are inserted (*cf.* fig. 231, p. 139). The shaft of each of these stigmas consists of elongated, succulent, colourless cells, whilst the barbs of the feather are extremely delicate and filamentous in character, and have the upper extremities of the cells of which they are composed continued as little papillæ (fig. 313 [2]). Neither in the main axis nor in the branches of the stigma are canals present. The cells fit edge to edge, and the pollen-tubes must bore a way for themselves in order to traverse the tissues in this case. The pollen-grains are attached to the papillæ, and as the little pollen-tubes are produced, these latter bend round so as to grow down along the inner face of the papilla. To do this they often execute very complicated curves, or they may grow spirally round the papillæ. Having reached the angle at the base of a papilla, they bore themselves a passage between the superficial cells and grow henceforward down to the ovary in an intercellular channel of their own making.

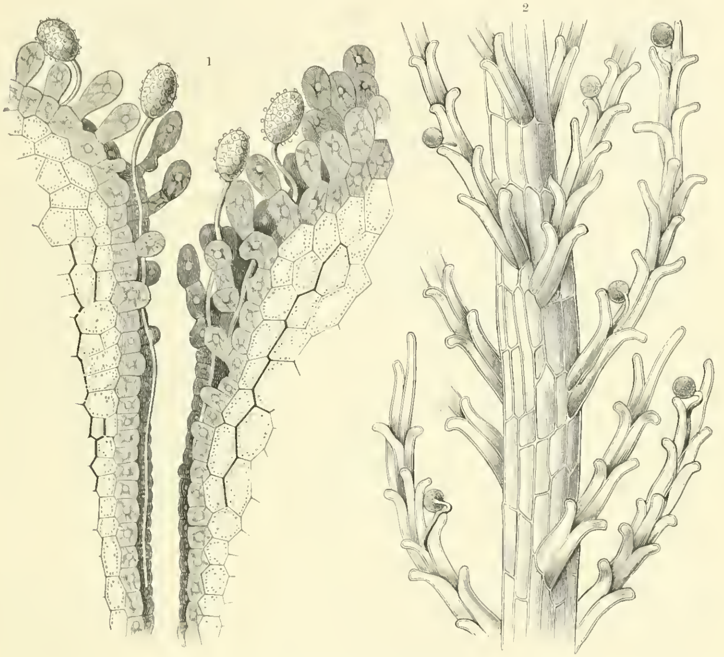

Fig. 313.—Development of Pollen-tubes.

[1] Longitudinal section of the stigma and upper portion of the style of *Lilium Martagon.* The pollen-grains present on the stigmatic papillæ are sending their tubes down the mucilaginous cells of the style-canal (after Dodel-Port); ×110. [2] Portion of the feathery stigma of *Avena elatior.* Pollen-grains are attached to the papillæ, and their tubes may be seen boring in between the cells of the stigmatic branches; × 170.

In the Grasses not only is no pre-existing canal present, but the cells between which the pollen-tube penetrates show no demonstrable difference from their neighbours. In this respect the Grasses differ from the very large number of plants which, although they do not possess an open style-canal as in *Lilium Martagon*, have a loose axial string of mucilaginous tissue in their styles through which the pollen-tubes readily penetrate. Examples of this condition are the Solanaceæ and Scrophulariaceæ. In other cases the conducting tissue is not differentiated from its surroundings, so that the whole of the substance of the style and stigma serves for the conduction of the pollen-tubes, as in *Cistus*, *Helianthemum*, and Orchids.

A curious condition prevailing in the Cactuses has been observed in the frequently mentioned *Cereus*. Here, although a narrow style-canal is present, the pollen-tubes prefer to make their way to the ovary embedded in the tissue surrounding the canal. From this it would appear that it is of advantage for the pollen-tubes to travel thus inclosed by other tissues.

Different again is the course followed by the pollen-tubes in the Malvaceæ and in many Caryophyllaceæ. The stigmas here are in some degree like those of Grasses. As there, so here, the superficial cells are produced into long, thin-walled papillæ; to these papillæ the pollen-grains become attached by the agency of insects. The pollen-tube as it develops from the grain at once perforates the wall of a stigmatic papilla and continues its growth in the cell-cavity. The course now followed is remarkable. In the Corn Cockle (*Agrostemma Githago*) the pollen-tube often zigzags from one side of the cavity of the stigmatic papilla to the other, not infrequently taking first of all the wrong direction and bending up towards the tip of the papilla, and then bending completely round again. Having reached the base of the papilla, the tube bores through into the conducting tissue in the interior of the style, but in its further course down to the ovary grows solely between the cells, not in them. It sometimes happens that more than one tube arises from a single pollen-grain; the accessory ones, however, are for purposes of firmer attachment, and though they occasionally enter a stigmatic papilla do not continue their growth down the tissue of the style. One functional pollen-tube only is produced from each pollen-grain. In the Malvaceæ (e.g. *Malva sylvestris*) the pollen-tube entirely fills a stigmatic papilla, broadening out at the base. Ultimately the contents of the tube escape from their membrane and travel down the style in an elongated mass, destitute of wall, like the plasmodium of a Myxomycete.

Whatever be the manner of its travelling, whether with or without a wall of its own, the aim of the protoplasm of the pollen-grain is to reach one of the ovules in the ovary. Having entered the cavity of the ovary, a pollen-tube shapes a course for an ovule. The particular portion of the ovule aimed at—in the vast majority of flowering plants—is the *micropyle* (*cf.* vol. i. p. 644), the little receptive spot at which the coats of the ovule are discontinuous, and at which access to the embryo-sac (wherein is contained the *egg-cell*) can be gained. Only comparatively rarely is the micropyle situated immediately below the point at which the pollen-tube must enter the ovary, as represented, for instance, in fig. 208[3], p. 74. Sometimes the micropyle is directed towards the side wall of the ovary, sometimes towards the central column, as in the Star of Bethlehem (*Ornithogalum*, figs. 315$^{3, 4, 5}$); whilst frequently the ovule is inverted so that the micropyle faces the base of the ovary (*cf.* fig. 211^{8}, p. 79). Since, in the majority of plants, several ovules are contained in a single ovary and each is fertilized by a separate pollen-tube, we find a number of tubes traversing the style, and, on their entering the cavity of the ovary, diverging to the several ovules. One would expect now to find this portion of the route to be followed by the pollen-tubes well indicated, either mechanically as by furrows and grooves, or by lines of secretory and nutrient cells leading to the micropyle. This, however, seems to be very rarely the case. As a rule such obvious guiding mechanisms are wanting. The pollen-tubes creep along the inner wall of the ovary to the places where the ovules are borne and then turn up and enter the micropyles, one pollen-tube to each ovule. The adjacent figure 314^{2} shows for a Rock-rose (*Helianthemum*) the whole course of the tubes from the stigma to the micropyles. As the tubes enter the cavity of the ovary they diverge and pass one to each ovule. A slight error, however, has crept into the figure in question in that the tubes are represented as passing *direct*

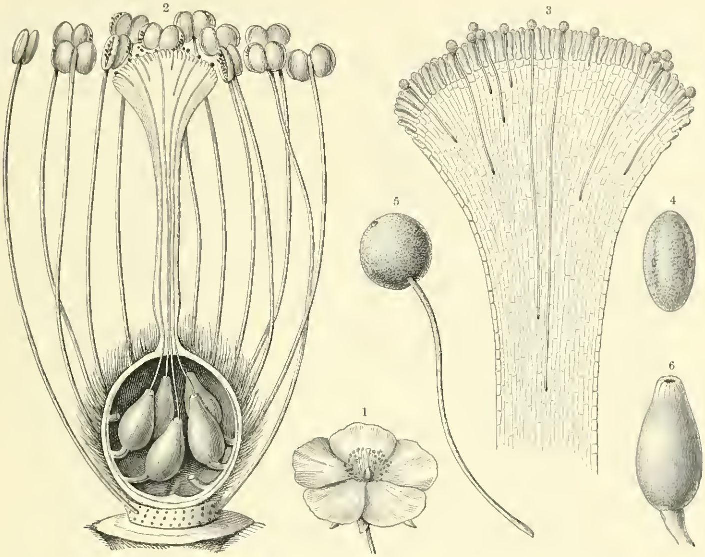

Fig. 314.—The course of the pollen-tubes in a Rock-rose (*Helianthemum marifolium*).

[1] A single flower, natural size. [2] A flower, stripped of its sepals and petals, showing stigma and style and ovary in longitudinal section; the pollen-tubes are seen passing down the style to the ovary and there going one to each ovule (the tubes are indicated erroneously as going direct to the micropyles; actually they follow a more devious course, first down the inside wall of the ovary and then up to the micropyles); ×22. [3] Stigma and upper portion of style in longitudinal section; shows pollen-grains attached to the stigmatic papillæ and tubes penetrating the tissues; × 55. [4] A dry pollen-grain; × 300. [5] A moistened pollen-grain developing its tube; × 300. [6] An ovule—which in this plant is of rather unusual form, the micropyle being at the end of the ovule distant from the point of attachment; ×50.

to the micropyles. In point of fact they follow a more roundabout course, creeping along the ovary wall, and then up the individual ovules to the micropyle.

It has been stated above that the pollen-tube enters the ovule *at the micropyle* in the vast majority of flowering plants. But this is not universally the case, as recent investigations have proved. In several of the trees belonging to the group of the Amentaceæ the pollen-tube follows an altogether different course. This was first established for the case of *Casuarina*, a curious switch-plant indigenous to Australia and certain parts of Eastern Asia. A small portion of a branch of this tree is shown in fig. 69 [5] (vol. i. p. 299). *Casuarina* is wind-pollinated, the flowers being unisexual, though both male and female flowers are borne on the same individual. The pollen-grains germinate in due course on the stigma, and their tubes traverse the tissues of the style. The tubes do not, however, enter the cavity of the ovary, but continue their growth immersed in the tissues of the ovary. They thus make their way to the points of insertion of the ovules, where they enter them, and at once travel to the base or *chalaza*. From the base of the ovule the pollen-tube penetrates towards the apex of the ovule, reaching the egg-cell from below, not from above as in cases in which the pollen-tube entered the ovule by the micropyle. This type of fertilization has been termed *chalazogamic* in contradistinction to the more usual micropylar or *porogamic* method. Quite lately a renewed examination of many common trees belonging to the Amentaceous group has shown that in several of them also fertilization is chalazogamic. This is the case in the Hazel (*Corylus*) and Hornbeam (*Carpinus*, fig. 314 A), belonging to the Corylaceæ, as also in the Birch (*Betula*) and Alder (*Alnus*, fig. 314 B), belonging to the Betulaceæ. In the Hazel and Hornbeam the pollen-tube, after reaching the base of the ovule, passes straight up to the egg-cell in the embryo-sac (*cf.* fig. 314 A, *p.t.*) in a manner similar to *Casuarina*, but in the Birch and Alder its course is

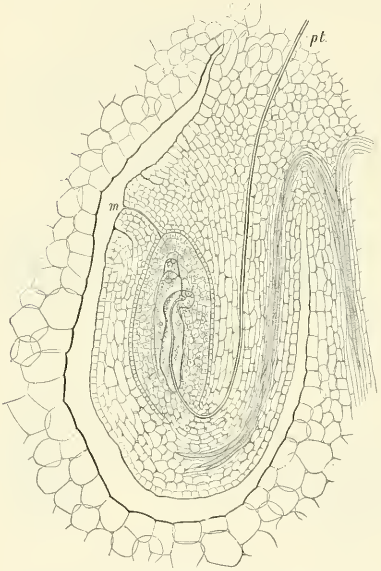

Fig. 314 A.—Chalazogamic fertilization in the Hornbeam (*Carpinus Betulus*).

The drawing shows a longitudinal section of an ovule almost filling the cavity of the ovary. The micropyle (*m*) and the two integuments are shown above the apex of the nucellus (in whose cells the nuclei are indicated). Within the nucellus three embryo-sacs are represented; a pollen-tube (*p.t.*), passing down into the substance of the ovule from the placenta, follows the course of the raphe and at the base of the nucellus (chalaza) bends sharply round and enters one of the embryo-sacs; its tip penetrates to the egg-cell at the apex of the embryo-sac. Much enlarged (from a drawing by M. F. Ewart).

not so direct. Here it passes by the embryo-sac on one side and then turns sharply down again, reaching the egg-cell from the same direction as it would have done had it entered by the micropyle (*cf.* fig. 314 B, *p.t.*). It is interesting to note that in many nearly allied Amentaceæ, as in the Cupuliferæ, which includes the Oak (*Quercus*), Beech (*Fagus*), and Chestnut (*Castanca*), fertilization is by the micropyle.

The following table indicates the method of fertilization as at present known in the various families comprehended in the group Amentaceæ:—

AMENTACEÆ.	*Mode of fertilization.*
1. Betulaceæ.	
Betula	Chalazogamic.
Alnus	
2. Corylaceæ.	
Hazel (*Corylus*)	Chalazogamic.
Hornbeam (*Carpinus*)	
Hop Hornbeam (*Ostrya*)	Not ascertained.
3. Cupuliferæ.	
Oak (*Quercus*)	Porogamic.
Beech (*Fagus*)	
Chestnut (*Castanea*)	
4. Juglandaceæ.	
Walnut (*Juglans*)	Porogamic.
Carya, *Ptero-carya*, &c.	Not ascertained.
5. Myricaceæ.	
Sweet Gale (*Myrica*)	Porogamic.
6. Casuarineæ	
Casuarina...	Chalazogamic.
7. Salicineæ.	
Willow (*Salix*)	Porogamic.
Poplar (*Populus*)	

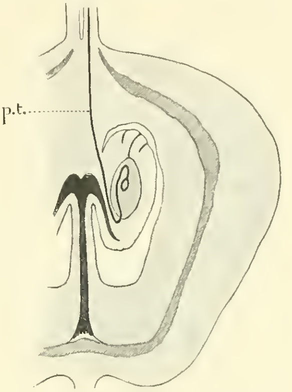

Fig. 314 B.—Chalazogamic fertilization in the Alder (*Alnus glutinosa*). Diagrammatic.

The drawing shows one half of a longitudinal section of the ovary. The wall of the ovary is thick, and has a hardened middle layer (shaded dark). At the top is the base of the style, from which the pollen-tube (*p.t.*) can be traced passing straight on through the substance of the ovary to the ovule. Entering the ovule by its point of attachment to the placenta the pollen-tube bends sharply upwards (at the chalaza) into the nucellus. It now passes by the small oval embryo-sac on the inner side, and when below the micropyle turns sharply down to the apex of the embryo-sac. The vascular supply of the ovules, which forms a column in the placenta, is shaded dark. Considerably enlarged (from a drawing by M. F. Ewart).

Many experiments have been made from time to time with a view to explaining the phenomena attendant on the wandering of the pollen-tube from the stigma to the micropyle. It has been shown that the pollen-tube is extremely sensitive to various external conditions, and that by appropriately varying these the direction followed by the tube in its growth may be controlled. Pollen-tubes are especially sensitive towards sugar-solutions, and bend out of their course towards the sugar. They also tend to grow away from the air, and show a preference for spaces saturated with aqueous vapour to such as are less humid. Of all the conditions which affect a pollen-tube, most conspicuous is the attraction which sugar exerts upon it. Various portions of the pistil exert a similar chemical stimulus on pollen-tubes, very marked being the action of the micropyle in this respect. A few of the experiments demonstrating this attractive property of stigma and ovules may be briefly described. If a fresh mature stigma be cut off and laid on a plate of gelatine, and the gelatine in its immediate neighbourhood be dusted over with pollen-grains of the same plant, in the course of a few hours, as the pollen-tubes are developed, it will be found that they converge upon the stigma in an unmistakable manner. Pollen-tubes, even at so considerable a distance from the stigma as seventy times their own diameter, have been observed to be influenced in this way. Similar results obtain when sections of a style are employed instead of a stigma, but the attraction is not so strong. Isolated ovules laid on the gelatine exert a very marked attraction upon pollen-tubes. In one case as many as forty pollen-tubes were counted converging upon the micropyle of an ovule of *Scilla patula.* Ripe ovules ready to be fertilized exert the strongest attraction, though younger and as yet immature ovules are not without influence.

Noteworthy is the fact that an ovule is found to attract not only pollen-tubes from pollen of the same species, but of others far removed from it in point of affinity. Thus the pollen-tubes of *Scilla patula* (a Monocotyledon) were found to be attracted by the ovules of *Diervilla rosea* and *Ranunculus acer* (Dicotyledons), tubes of *Primula sinensis* by the ovules of *Antirrhinum majus* and *Digitalis grandiflora,* those of *Hesperis matronalis* by ovules of *Lonicera Periclymenum,* &c. In these experiments these strange pollen-tubes were not only attracted towards the micropyle, but actually in a few cases penetrated it. Still, no suggestion is made that anything of the nature of fertilization could be accomplished by these foreign pollen-tubes.

Nor is this attraction limited to pollen-tubes. The delicate hyphæ of several mould-fungi are similarly attracted, as also, when the surface on which the ovule rested was moistened, was that common micro-organism of decomposition, *Bacterium Termo.*

Thus it appears that substances are present in the stigma, style, and ovules, which exert a chemical attraction upon pollen-tubes, gradually leading them to the micropyle. Though it has not been possible to determine in all cases what these substances are, it is extremely probable that they are of a sugary nature. In the case of plants with chalazogamic fertilization, in which the pollen-tube, as we have seen, never enters the cavity of the ovary, it would be of interest to ascertain if the micropyle is destitute of attraction for pollen-tubes.

As stated, the attraction exerted by a given ovule or portion of a pistil is not limited to pollen-tubes of the same species, but seems common to pollen-tubes in general, and indeed to fungal hyphæ and the like. Thus it happens that instances are recorded in which fungal spores fell on the stigma, and germinating there, sent their hyphæ down the style to the ovary like pollen-tubes. And so with foreign pollen. Though it is often stated that the pollination of the stigmas of a plant A with pollen from B (a plant not allied to A) is *without result,* what is actually indicated is that no seed has been ripened by the pistil thus pollinated. Experiment has shown that, just as the pollen-tubes of one plant may be attracted towards the micropyle of an ovule of a plant of entirely different family, so pollen will germinate on the stigma of a similarly remote plant and form tubes which penetrate considerable distances down the style, though they perish eventually. Still even should these foreign pollen-tubes actually get access to the micropyle, a fertilization of the egg-cell by the foreign spermatoplasm would be impossible, owing to the inability of the sexual protoplasm to combine outside a very narrow range of affinity. We have already seen that many plants can be fertilized either by pollen from another flower of the same species, or, wanting this, by their own pollen. Both categories of pollen-grains are competent to develop tubes and to fertilize the ovules. Under these circumstances it would be very interesting to know what exactly happens when pollen-grains of both these categories are present on one and the same stigma; whether (as is probable) both develop pollen-tubes, whether both

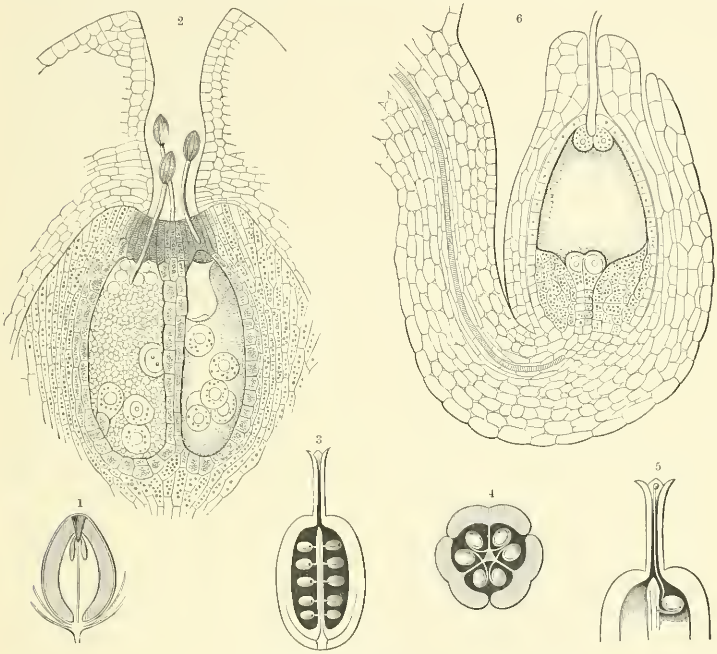

Fig. 315.—Fertilization.

[1] Longitudinal section through the ovule of *Ephedra* (a Gymnosperm); ×3. [2] Apical portion of a longitudinal section of the ovule of *Ephedra*, showing the pollen-grains in the micropyle producing their pollen-tubes; ×100. [3] Longitudinal section through the ovary of *Ornithogalum nutans*; × 2. [4] Transverse section of the same ovary; × 3 [5] Longitudinal section through stigma, style, and upper portion of ovary of *Ornithogalum* showing a pollen-grain on the stigma with its pollen-tube passing down the style-canal to the micropyle of an ovule; × 3. [6] Longitudinal section through an ovule of *Ornithogalum*. The funicle or stalk of the ovule is seen to the left, the ovule proper to the right. In the latter there is a large central space, the embryo-sac which contains certain small cells; towards the apex two together of which one is the egg-cell and the other a synergida, at the base two antipodal cells are represented. Around the embryo-sac is a layer of nucellar tissue one cell thick, whilst below, this tissue is more bulky (contents dotted). Around the nucellus are the integuments. A pollen-tube has grown down the micropyle and perforated the apex of the embryo-sac. It is represented in contact with the egg-cell and one synergida. The other synergida is not shown; ×100. (Partly after Strasburger.)

sets of tubes reach the ovary, or whether one set receives a check of some sort. In fact we want to know whether foreign pollen is prepotent over own pollen (where both are competent to fertilize), and if so how the prepotency is accomplished. This and a host of similar problems await solution.

Passing on now to the union of spermatoplasm and ooplasm it is first of all necessary to describe the structure of the ovule in some detail. The egg-cell which has to be fertilized forms but a small portion of the ovule. It is produced in Flowering Plants within a large cell prominently developed and termed the *Embryo-sac.* This embryo-sac is one of the cells of the central portion of the ovule known as the *Nucellus,* and this cell as the time of maturation of the ovule approaches grows much in size, in part at the expense of its neighbours. Ultimately the embryo-sac occupies a large portion of the nucellus, being still inclosed by a layer of small nucellar cells. Outside this are the integuments. They are not completely closed, but at one spot an opening (the *micropyle*) is left, the entrance by which the pollen-tube gains access to the embryo-sac. The general relations of the embryo-sac to the other portions of the ovule are shown in fig. 315^6, a longitudinal section of the ovule of *Ornithogalum.* In fig. 316 three stages of the embryo-sac of *Monotropa* are shown just at the time of fertilization. At an earlier stage the embryo-sac is a uni-nucleate cell, and before the arrival of the pollen-tube at the micropyle its contents divide up into a number of small cells, which, though devoid of cell-membranes, are readily distinguishable from one another. At the apical or micropylar end three of these cells are situated. The two uppermost, side by side, are known as the *synergidæ,* whilst close below them and slightly to one side (*cf.* fig. 316) is the egg-cell, destined to be fertilized. These three cells constitute the "egg-apparatus". At the other extremity of the embryo-sac, *i.e.* at the base, three cells are present which are known as the *antipodal* cells. These, soon after their formation, develop walls around themselves and appear to play no part in subsequent phenomena. Besides these, there are two nuclei (the so-called *polar* nuclei) lying in the protoplasm of the embryo-sac, one close above the antipodals, the other just below the egg-apparatus (fig. 316^1). These two approach one another at about the moment of fertilization and fuse (figs. 316^2 and 316^3) about midway between egg-apparatus and antipodals. They give rise ultimately to the food-material which nourishes the young fertilized egg-cell during its early stages of development.

The egg-cell and its attendant synergidæ contain each a well-marked nucleus and vacuoles. In the egg-cell the vacuole is above the nucleus (fig. 316^3), in the synergidæ the vacuoles are below the nuclei (fig. 316^2). The nucleus of the egg-cell is often very large. The structure and changes of cell-nuclei have already been briefly reviewed at vol. i. p. 581.

Meanwhile, in the pollen-tube changes have also taken place. Actually in the pollen-cell before the pollen-tube is produced two nuclei are present. Though both of these enter the tube one is quite sterile and soon atrophies. The other, however, surrounded by a small portion of protoplasm, but destitute of wall, constitutes the male sexual cell. It is carried, embedded in the general protoplasm of the pollen-tube, near the tip, and so is gradually brought down to the embryo-sac. Usually this male cell divides into two, but there is no evidence to show that more than one of the daughter-cells thus produced takes an actual part in fertilization. When the tip of the pollen-tube reaches the micropyle (as in fig. 315^6, though the contained male cells are not shown), the male sexual cells are well up to the end of the tube. The pollen-tube forces its way down the micropyle, and perforates the apex of the embryo-sac. The tip of the tube is now opened, and a male sexual cell passes out, and, traversing the synergidæ, enters the egg-cell. The synergidæ seem to promote this transfer of the male cell to the egg, though the precise part played by them is not fully understood. With the passage of the male cell the synergidæ collapse and shrivel; their part is played. The anterior of the two male cells of the pollen-tube enters the egg-cell, the other one being possibly of the nature of a reserve in case of accident. Occasionally, it also enters, and has been observed in the egg, though probably this is an accidental circumstance. After the entrance of the male cell its nucleus approaches the female (egg-) nucleus and fuses with it. This fusion constitutes the act of fertilization. Though this nuclear fusion is the most characteristic feature of fertilization it may well be that the other elements which enter the egg-cell with the male nucleus likewise fuse with the protoplasm of the egg. So far, observations have not absolutely determined the fate of these less conspicuous elements. On the other hand, it is possible that these subordinate elements serve in large part merely as food-material for the egg. As yet the time has not arrived to speak decisively on these points.

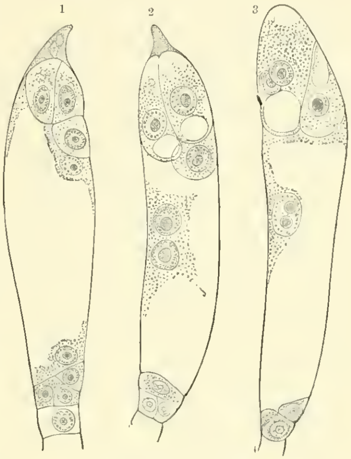

Fig. 316.—Embryo-sac of *Monotropa*.

Three stages are shown just preceding fertilization, in the order $^{1, 2, 3}$. In each of them we see the group of antipodal cells at the base, and the egg-apparatus at the apex. ^{1} and ^{2} show the two synergidæ side by side and the egg-cell adjacent to them. In ^{3} the synergidæ are on the left, seen through one another, both their nuclei showing; the egg-cell on the right. The process of fusion of the so-called polar nuclei is shown in the figs.; in ^{1} they are not yet detached from their respective groups, in ^{2} they have approached one another, in ^{3} they are in process of fusion.

The fertilized egg-cell, which we may now term the *embryonic cell*, soon gives indication of the change which it has undergone. It secretes a cell-wall around itself. Had it not been fertilized the egg-cell would have remained naked and inactive, and ultimately would have perished.

In the account of fertilization of the Angiosperm just given, the main facts have been related; and although from time to time fresh observations come to light, it is hardly probable that the main outlines as given above will be overthrown. That a fuller knowledge of the details will be obtained is exceedingly probable, in view of the active state of research into these processes.

In the *Gymnosperms*, the group of Flowering Plants with exposed ovules, though the essential facts of fertilization—the fusion of the male sexual cell with the female sexual cell (egg)—are the same as in the *Angiosperms*, just described, in many subordinate points they exhibit marked differences. The male flowers of Gymnosperms produce stamens with anthers in which pollen-grains are developed much as in Angiosperms. The arrangements, however, associated with the production of ovules are simpler than in the Angiosperms, and recall to some extent the characters presented by certain Ferns. In the Ferns and other Cryptogams it will be remembered that fertilization is under water, whilst in Phanerogams this is accomplished through the medium of the air (*cf.* p. 71). The spermatozoids of the Cryptogams reach the egg-cell in the oogonium or archegonium by swimming; they are naked protoplasmic masses, and need no enveloping and protective cell-wall. It is otherwise in the Phanerogams, where aërial fertilization obtains. Here a membrane around the spermatoplasm is of great value; it serves to protect the contents of the pollen-grain during its journey through the air, and afterwards, in connection with the pollen-tube, is of the utmost value in conveying the male sexual cell to the egg. Notwithstanding the resemblance presented by the female flowers of many Gymnosperms to certain Cryptogams, they agree with the Angiosperms in the fact that the male cell is brought to the egg-cell by means of a pollen-tube. In this point all Gymnosperms agree, *i.e.* the Cycads, Conifers, and Gnetaceæ.

The ovules of Gymnosperms show the grosser characters of those of Angiosperms. In fig. 335 [7] is shown a scale from a female flower (cone) of the Scotch Pine (*Pinus sylvestris*). Right and left at its base are the ovules, two in number. Each ovule exhibits a central nucellus and a conspicuous integument surrounding it, leaving a wide, funnel-shaped micropyle giving access to the tip of the nucellus (*cf.* also fig. 208 [8], p. 74, representing an ovule of *Cycas*). Within the nucellus a large cell becomes marked out, as in Angiosperms; this is the embryo-sac. The embryo-sac becomes filled with an extensive tissue, the endosperm, and produces at its apical end (towards the micropyle) a number of egg-cells. These vary in number from 2–15 in various Gymnosperms, but in any case they are all assembled together beneath the micropyle. Associated with each egg-cell is a neck, recalling that structure in the archegonium (or amphigonium) of Ferns (*cf.* p. 67). Fig. 315 [2] shows the tip of a gymnospermic ovule in section, considerably enlarged. Note the funnel-shaped micropyle (with germinating pollen-grains in it) and two large, oval egg-cells in the endosperm below. The slight shading above the tips of the two egg-cells indicates the necks. The contents of the egg-cells in this figure have already given rise to several cells, as in the stage represented fertilization has just occurred. The cells here shown in *Ephedra* (fig. 315 [2]), or in most other Gymnosperms a limited number of cells (often four) cut off at the base of each egg-cell, develop into little embryos, of which, however, ultimately one only survives for each seed. A characteristic feature, occurring shortly before fertilization, is the cutting-off of a small cell from the summit of the egg-cell. This little bi-convex cell (shown at the tip of the right-hand egg in fig. 315 [2]) is known as the "ventral canal-cell". A similar cell is cut off in the Ferns, &c., and lies at the base of the neck of the archegonium just above the egg-cell. It is afterwards absorbed.

From a comparison of the structures in the ovule of a Gymnosperm with those arising on the Fern-prothallium, or Moss-plant, it seems probable that the egg-cell, with its neck in the former, corresponds to the archegonium of the latter, though the archegonium in the Gymnosperm is somewhat reduced when compared with the exposed archegonium of Ferns and Mosses.

The number of egg-cells (=archegonia) produced in the ovule of a Gymnosperm is various. In the Spruce Fir and Pine there are from 3 to 5, in the Cypress and Juniper 5 to 15. In the Firs and Pines the egg-cells are well isolated from one another by layers of endosperm, in which they are embedded; in Cypresses and Junipers the egg-cells are all in immediate contact, forming a rosette-like cluster at the top of the endosperm under the micropyle. The tissue in which they lie embedded, the endosperm, is in Gymnosperms pretty extensive, and being well-stocked with food-materials, forms, after fertilization, a nutritive bed for the young developing embryos, and is ultimately absorbed by them.

In the Angiosperms, on the other hand, the ovules are not exposed on open scales, as in Gymnosperms, but inclosed in definite chambers, the ovaries. Pollen is brought to the stigma (not to the micropyle, as in Gymnosperms), and fertilization is accomplished by the development of pollen-tubes, which penetrate the tissues of the style to the ovules. In Gymnosperms there are no ovaries or styles or stigmas. Pollen is brought by the wind direct to the micropyle of the ovules. Various arrangements exist for bringing the pollen-grains into the micropyle and for holding them there. Just at the time when pollen is liberated from the male flowers the micropyle is opened wide, and its lining cells are rendered sticky by a mucilaginous secretion, so that the pollen brought by the wind sticks to it. This mucilage often projects as a little droplet from the micropyle, and in it the pollen-grains are caught; as this drop gradually dries up and contracts the pollen-grains are sucked into the micropyle, so that the grains come to lie right on the tip of the nucellus of the ovule, from which point they germinate, putting out their tubes (*cf.* fig. 315 [2]). These drops of mucilage can be well seen in early spring on the exposed ovules of the Yew-tree (*Taxus baccata*). This plant is diœcious, and on the female plants the tips of the ovules project from a few scale-like wrappings, which envelop the base of each ovule (*cf.* figs. 336 [2] and 336 [3]). At the time when the male flowers are intrusting their pollen-grains to the wind (usually in March) one may see the female plants, on a sunny morning sparkling in the sunshine as it were with dew-drops. These "dew-drops" are in reality droplets of mucilage, excreted from the micropyles of the ovules, awaiting the chance deposition by the wind of pollen-grains. By and by they dry up and the entangled grains are sucked into the micropyle. In Gymnosperms it is the micropyle, not the stigma, which is pollinated.

After the entrance of the pollen-grains into its mouth the micropyle contracts somewhat, so that the pollen is, so to speak, imprisoned. In Gymnosperms the active development of pollen-tubes only occurs some considerable time after pollination. In the Pine the pollen-grains put out short tubes soon after pollination, but these tubes remain dormant from the spring in which pollination takes place through the summer, autumn, and winter, and only continue their growth after the lapse of about a year. Meanwhile changes take place within the ovule leading to the production of the archegonia with mature egg-cells. Actual fertilization occurs about thirteen months after pollination.

The contents of the pollen-cell, before it leaves the anther (Pines and Firs), or shortly after its reception in the micropyle (*Taxus* and *Cupressus*), divides several times, a number of small cells being cut off at one side of the grain and their substance being separated from the rest of the contents of the grain by cell-membranes. Of these small cells one is the male sexual cell, and ultimately effects fertilization. The big cell (known as the "vegetative cell") produces the pollen-tube. The male sexual cell ("generative cell"), becoming free from its attachments (membranes), passes into the pollen-tube, where it divides into two cells. Ultimately one of these cells fertilizes an egg-cell (the other not being required). In the Juniper, where one pollen-tube fertilizes more than one archegonium, both these generative cells—and possibly others, the result of their further division—would appear to be utilized. The generative cells are carried along with the tube near its growing tip—much as in Angiosperms. Bit by bit the pollen-tube penetrates deeper into the substance of the ovule which forms the floor of the micropyle. Ultimately the tube reaches the neck of an archegonium, and pushes in between the neck-cells, carrying the male cells to the mature egg-cell. In the Cypress and Juniper, where several egg-cells are clustered close together, the tip of the tube widens out, sending a little branch to each of the egg-cells (archegonia), every one of which it is competent to fertilize. In the Pine, Firs, and other Gymnosperms, distinct tubes from separate pollen-grains penetrate to the several archegonia.

Fertilization happens much as in Angiosperms (described on p. 417); the male cell enters the egg-cell, and the male nucleus fuses with the female nucleus. Probably the other elements of the male cell are also taken up by the egg-cell. Indeed, the whole process of pollen-tube development and fertilization is exceedingly similar to these events as described in the Angiosperms. A chief point of difference consists in the absence of distinct cell-walls between the cells which arise in the pollen-grain of the last-named group.

The *development of the embryo from the fertilized egg-cell* is different in Angiosperms and Gymnosperms. In *Angiosperms* the egg-cell, after surrounding itself with a cell-wall, becomes partly attached to the apex of the embryo-sac. It divides by a transverse wall into two cells, one directed towards the micropyle, the other towards the base (chalazal end) of the embryo-sac. The upper (*i.e.* micropylar) of these two cells stretches, and is repeatedly segmented; thus a string of cells is formed, known as the *suspensor*, bearing at its lower extremity the *embryo-cell*, which gives rise to the greater portion of the young plant. The suspensor, by its elongation, brings the embryo-cell well down into the cavity of the embryo-sac, where it is embedded in the substance of the endosperm which has meanwhile developed. The nutrition of the young plant is thus assured during its early stages. In many Parasites and in Orchids the full-grown embryo shows but little differentiation, and is little more than a mass of cells exhibiting no distinction of stem and leaf-structures; but in the great majority of Angiosperms it soon shows a differentiation into parts—into a little root at one end and a stem at the other, with the rudiments of leaves (*cf.* vol. i. p. 599, figs. 141 [1] and 141 [2]). These leaves, the *cotyledons*, are a conspicuous feature of the embryo, and in several plants they are coloured green by a precocious development of chlorophyll in their tissues (e.g. *Styphnolobium japonicum*). In a large number of plants, as, for instance, the Apple and Oak, Bean and Pea, garden Nasturtium (*Tropæolum*) and Water Chestnut (*Trapa, cf.* vol. i. p. 607, figs. 144 [1, 2, 3, 4, 5, 6]), the cotyledons become much enlarged and succulent, and take up large quantities of food-material, which remains stored up in them as reserve-material for the further development of the young plant at germination. When this happens the cotyledons usually come to fill the whole cavity of the seed right up to the integument (*testa*). In the majority of plants, however, the cotyledons remain small and thin, and do not take up the whole reserve of food-material which envelops the embryo. Under these circumstances the embryo is provided with a special reserve-tissue, destined for its consumption when it is separated from the mother-plant. This tissue is analogous to the yolk of a bird's egg, and consists of a tissue of cells filled with fat, starch- and proteid-granules. This food-tissue is variously known as *endosperm, albumen,* &c., but the terminology associated with it does not reflect great credit upon the Botanists who are responsible for the introduction of the various terms.

The starting-point for this *reserve-tissue* consists of the nucleus which arises in the embryo-sac from the fusion of the so-called *polar nuclei* (represented in figs. 316 [1, 2, 3], and described on p. 416). Around these nuclei a certain amount of protoplasm collects, and after their fusion into the so-called *definitive nucleus* (fig. 316 [3]), a very active cell-division sets in, which results in the formation of a parenchymatous tissue which occupies the embryo-sac and becomes filled with food-materials (fat, starch, and proteids). This tissue is the already-mentioned *reserve-tissue* of the seed or *endosperm*. Most frequently, as we have stated, the embryo enters on a resting period embedded in or adjacent to this reserve, and absorbs it at germination. In other cases, as in the Bean, Oak, &c., as mentioned, the cotyledons of the embryo forthwith take up all this food, so that when the resting-stage comes on, the greatly swollen embryo fills the whole cavity of the seed. This former class of seed is spoken of as *albuminous*, the latter as *ex-albuminous*. There is just this difference between albuminous and ex-albuminous seeds: in the former the embryo only takes up the food-material at germination, in the latter, relatively early, before the seed enters on its resting-stage. The ultimate fate of the food-material is the same in both cases, *i.e.* to nourish the young plant.

The relations of the *embryo* to its *reserve-tissue* are very various. In many plants, *e.g.* Pimpernel, Wood Sorrel, Snapdragon, and Strawberry-tree (*Anagallis, Oxalis Acetosella, Antirrhinum majus, Arbutus Unedo, cf.* figs. $317^{3, 4, 5, 6, 7, 8, 9, 10}$), the straight embryo lies embedded in its reserve-tissue. The same relations obtain in the Rue (*Ruta graveolens, cf.* figs. 317^{1} and 317^{2}), the embryo here being slightly bent; whilst in *Phytolacca decandra* (fig. 317^{11}), on the other hand, the embryo is outside its reserve-tissue, and curved around it like a horse-shoe. In Sapindaceæ and Chenopodiaceæ the embryo is spirally twisted. In the Grasses it is laterally placed to its reserve-tissue (*cf.* vol. i. p. 599, figs. 141^{3} and 141^{4}), and the manner in which it utilizes its reserve has been already fully described in vol. i. p. 604.

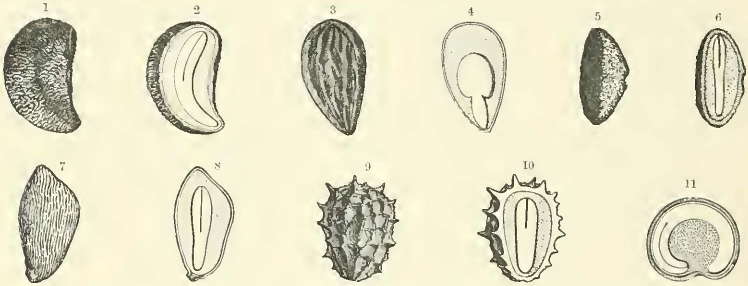

Fig. 317.—Seeds with a Reserve-tissue.

^{1} *Ruta graveolens*, the intact seed. ^{2} Longitudinal section of the same. ^{3} *Oxalis Acetosella*, intact seed. ^{4} Longitudinal section of the same. ^{5} *Anagallis phœnicea*, intact seed. ^{6} Longitudinal section of the same. ^{7} *Arbutus Unedo*, intact seed. ^{8} Longitudinal section of the same. ^{9} *Antirrhinum majus*, intact seed. ^{10} Longitudinal section of the same. ^{11} Longitudinal section of seed of *Phytolacca decandra*. (After Baillon.)

Both the embryo and its reserve-tissue increase at the expense of the tissue immediately external to the embryo-sac; and in the ripe seed very slight traces of this tissue are to be found. Only in relatively few seeds is food stored in this peripheral tissue (*i.e.* in the tissue of the nucellus between the integument and embryo-sac). Under these circumstances this nucellar tissue assumes very much the character of the more usual reserve-tissue (endosperm) which is formed *within* the embryo-sac. Its cells become filled with fat, starch, and proteids, which serve later on as food-material for the young plant. Reserve-tissue when stored *within* the embryo-sac is termed *endosperm*; this, which arises external to the embryo-sac is, in contradistinction, termed *perisperm*.

It is worthy of note that a formation of reserve-tissue does not take place in ovules which are not fertilized. The act of fertilization obviously exerts an influence not limited to the embryo. One may compare this influence to the impulse generated when a stone is thrown into still water. Just as waves travel in ever-widening circles from the centre of disturbance, so it is with the changes in the ovule: first, changes are noticeable in the egg-cell, then successively in the embryo-sac, integuments, in the carpels, and, finally, in the flowering axis which bears the whole of the structures concerned. These changes, which become manifest in the form of growth, are executed on a definite plan in every plant, and depend on the peculiar constitution of the protoplasm. The aim of these growth-changes is not difficult to determine. The new organism which has arisen from fertilization must be adequately provided for the future; it is detached sooner or later from its parent-plant, and has to establish itself in a new place. The embryo requires special equipment for its journey and for its start in life; it requires a means of dispersal and protection against attacks from animals so long as it remains attached to the parent-plant, it requires also protection against unfavourable climatic conditions. These various equipments are provided by peculiar changes in the integument, carpels, and receptacle, changes which are initiated at fertilization.

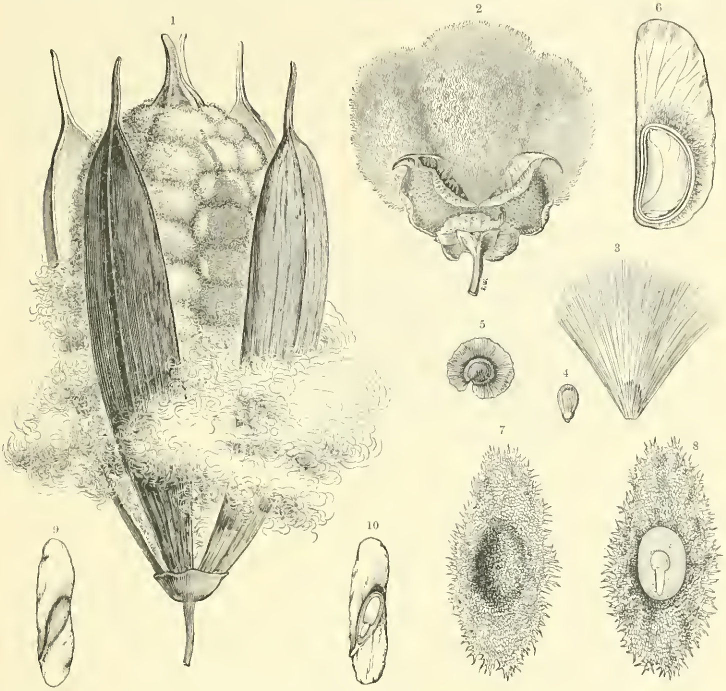

Fig. 318.—Seeds with winged and hairy appendages.

[1] Dehiscent fruit of *Eriodendron*; the seeds embedded in a hairy investment are visible between the valves. [2] Dehiscent fruit of *Gossypium herbaceum*; the mass of seeds is contained in a hairy investment protruding from the valves. [3] Seed of Aspen (*Populus tremula*) with silky appendage. [4] The same seed stripped of its silk. [5] Winged seed of *Lepigonum marginatum*. [6] Longitudinal section of the winged seed of *Vochysia*. [7] Winged seed of *Cinchona*. [8] Longitudinal section of this seed. [9] Winged seed of *Cedrela Toona*. [10] Longitudinal section of same. [4–8] magnified. (Partly after Baillon.)

The integuments of the ovule are altered into the *seed-coat*, which often exhibits a differentiation into two layers. The inner layer takes the form of a delicate, colourless membrane which is rarely hardened, or of a mucilaginous, readily-swelling layer. The outer seed-coat or *testa* shows, however, a great variety of form. It usually consists of several layers of cells, the successive layers of which are frequently very differently fashioned. Sometimes they are soft and membraneous, sometimes rigid and parchment-like, woody or horny, whilst in other cases they may be succulent and fleshy, or converted into a mucilaginous, sticky envelope. The outmost layer of the testa is usually brown, gray, and black, more rarely yellow, white, or red in colour. The significance of the various slimy layers, which on moistening become sticky, of the little pits and furrows, warts, spines, and the like in promoting the firm anchoring of the seed on its germinating bed has already been fully pointed out (*cf.* vol. i. pp. 614–620). Many seeds, in order that they may be distributed by the wind, develop from the outmost layer of the testa wing-like appendages, as, for instance, in the seeds of the Caryophyllaceous *Lepigonum marginatum* (see fig. 318 [5]), in those of the Cinchona-tree (*Cinchona*, figs. 318 [7] and 318 [8]), in the tropical *Vochysia* (fig. 318 [6]) and *Cedrela* (figs. 318 [9] and 318 [10]), and many others. This just-mentioned *Vochysia*-seed is also characterized by the curious wrapping of the cotyledons upon one another (fig. 318 [6]). Often, again, for the same purpose, the superficial cells of the testa grow out, forming a plume or plexus of silky or cottony hairs, as in the Indian species of Cotton-plant (*Gossypium herbaceum*, fig. 318 [2]), and in the cotton-producing *Eriodendron* (fig. 318 [1]). In the seeds of the Oleander (*Nerium Oleander*) the hairs at the apex are longer than those at the base, whilst in the Willow-herb (*Epilobium*) a delicate tuft of long silky hairs is developed at the apex only.

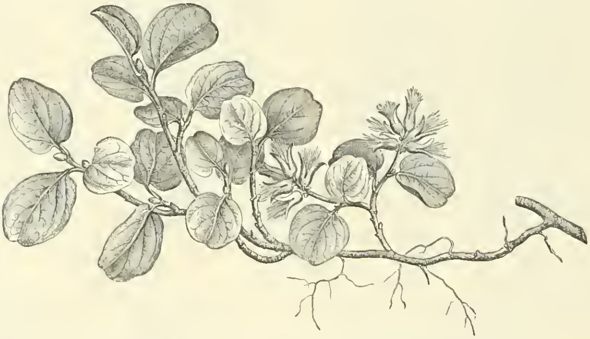

Fig. 319.—*Salix polaris* with opened fruits showing masses of hairy seeds escaping.

In a considerable number of plants there is developed from the base of the seed, or from its funicle, a curious and special structure, which by the time the seed is ripe envelops the seed like a mantle. This structure is known as the *Aril*. These arils show very various characters, just as the testa itself may do. In the Willow (*Salix*, fig. 319) and Poplar (*Populus*, figs. 318^3 and 318^4) it consists of long, delicate silky hairs; in many Passifloraceæ, Sapindaceæ, and Celastrineæ—amongst others, in the well-known Spindle-tree (*Euonymus*), it forms a fleshy, succulent investment, often coloured bright red or orange, whilst in the Myristicaceæ it forms a curious, laciniated sheath. In the Nutmeg (*Myristica moschata*) the seed proper constitutes the nutmeg of commerce, whilst the mace is the aril which grows around this seed. When these accessory structures of the seed are only developed locally as little ridges or bumps at the base of the seed, or on the funicle, they are known as *caruncles*. A well-marked, fleshy cock's-comb-like caruncle is formed on the seeds of the Celandine (*Chelidonium majus*). When the swelling is limited to the point of attachment of the seed to its funicle, one speaks of a *hilar caruncle*, as is seen in the Pansy (*cf.* figs. 320^1 and 320^2). The spot where the seed is attached to its stalk is known as the *hilum*, and is readily seen, even when distinguished by no special swelling or caruncle, on a detached seed. It is usually a well-defined area, coloured differently from the rest of the testa, sometimes projecting, sometimes slightly excavated, and not infrequently having the form of a well-marked groove (see fig. 320^5). At the place where separation has occurred there is a kind of scar, the *hilar scar* (sometimes called the *omphalodium*). The spot occupied by the micropyle is often recognizable on the ripe seed, and may be termed the *micropylar scar*. It usually appears as a little hole or pin-point depression bordered by peculiar tissue. In curved (campylotropous) seeds, the micropylar and hilar scars are seen near together, but not so close as to be inseparable (figs. 320^6 and 320^7; in 320^6 the point indicates the position of the micropylar, the excavation that of the hilar scar). In the Castor-oil plant (*Ricinus communis*, figs. 320^3 and 320^4), the lips of the micropyle undergo considerable growth, forming a little cushion or micropylar caruncle, very conspicuous at the top of the seed.

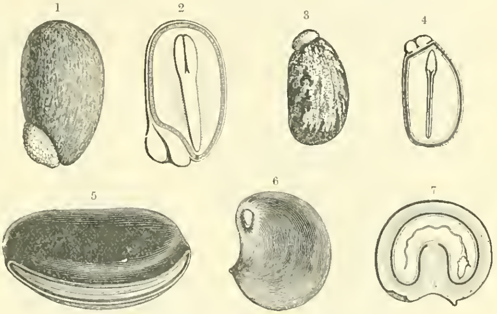

Fig. 320.—Seeds with caruncles and hilar scars.

^{1} Seed of *Viola tricolor*. ^{2} The same in longitudinal section. ^{3} Seed of *Ricinus communis*. ^{4} The same in longitudinal section. ^{5} Seed of *Physostigma venenosum*. ^{6} Seed of *Anamirta Cocculus*. ^{7} The same in longitudinal section. (After Baillou.)

Corresponding to the externally visible hilar and micropylar scars is a curious internal structure of this portion of the seed-coat. This will be more intelligible when it is explained that in many cases the water needed by the resting embryo for its further development can only be absorbed at these spots. The tissue here, indeed, serves as a mechanism for supplying the embryo with moisture from the germinating bed. For its successful operation it is necessary that the seed should be favourably situated upon the soil, in other words, that these portions of tissue which conduct water to the embryo should be in contact with the damp earth. Such a position is promoted by the fact that in cases of the kind under discussion the seed is so formed and its centre of gravity so adjusted that in falling the hilar scar generally comes to lie underneath. The tissue here is more or less porous and provided with lacunæ, so that water can be taken up and transmitted to the embryo. Not infrequently it consists of loose stellate cells, and water is absorbed from the environment as by a sponge and placed at the service of the deeper-lying regions of the seed, especially the embryo.

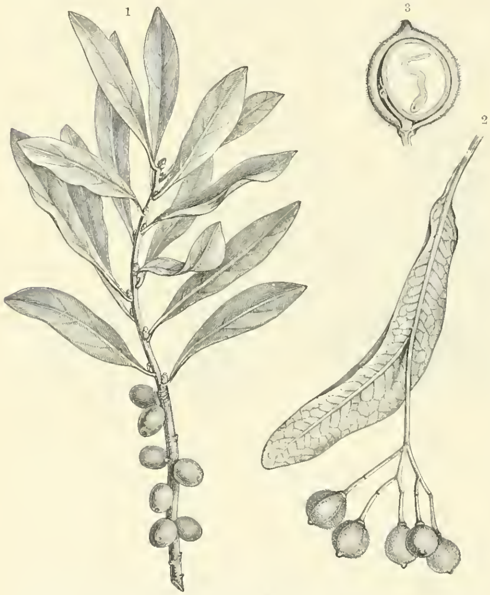

Fig. 321.—^{1} Branch of Mezereon (*Daphne Mezereum*) with berries. ^{2} Fruiting branch of the Lime (*Tilia*) with downy hairs investing the nut-like fruits. ^{3} Longitudinal section through a fruit of the Lime. ^{1} and ^{2} natural size. ^{3} magnified.

In those seeds, on the other hand, in which water is not absorbed at definite spots but over the whole surface, there exist scattered over the surface between the thickened impervious cells, which form the greater portion of the investment, special strings of cells or minute canals which at the proper time are permeable and serve for the taking up of water. Thus, for instance, in the hard, round, black seeds of the Indian Shot (*Canna*), the testa, consisting as it does of an outer layer of thick-walled palisade-cells with several layers of transversely-stretched stony cells beneath, constitutes an exceedingly strong protection for the embryo. But over the whole surface of the seed are distributed tiny depressions, at the base of each of which a stomate opens. Each of these stomates leads into a canal of minute proportions traversing the layers of the testa and adequate for taking up water at germination.

Intimately connected with the developing seeds is the structure in which they are contained, and in which they were originally fertilized. This is known at the time of fertilization as the *pistil* or *ovary*, and later, when the seeds are ripe, as the *pericarp, seed-capsule,* or *case.* As a rule this structure is known to Botanists as the *fruit,* though this designation is open to criticism. In the broad sense the fruit in Phanerogams should include everything which undergoes alteration after fertilization either in the flower or flowering axis. All these changes take place in the parts in question for the purpose of promoting the interests of the embryo, and properly equipping it when the time comes for its severance from the parent plant, consequently the whole of the structures which participate in this object should be regarded as the fruit. From this point of view the seed-case or pericarp (derived from the pistil) constitutes only a portion of the fruit. Since, however, the seed-case in a very large number of cases approximates to and essentially constitutes the whole fruit, we will not press our quarrel with the descriptive botanists to the point of pedantry, but having made our protest fall into line with the usual terminology.

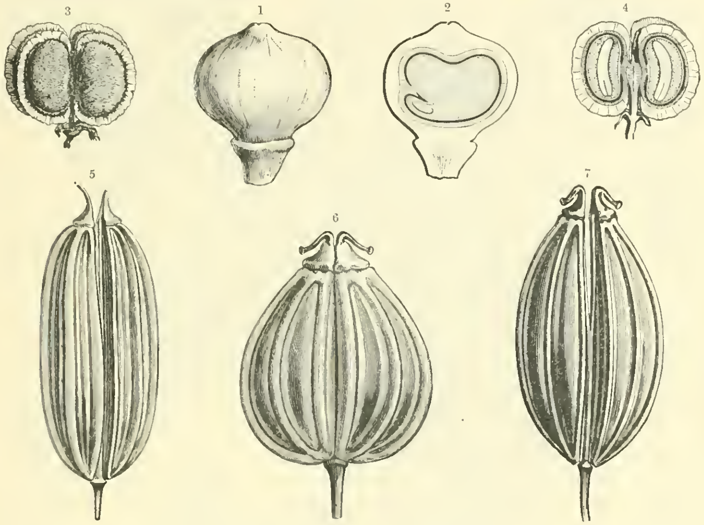

Fig. 322.—Indehiscent fruits and schizocarps.

[1] Drupaceous Nut of *Fumaria.* [2] The same in longitudinal section. [3] Indehiscent fruit of *Callitriche.* [4] The same in longitudinal section. [5] Schizocarp of *Fœniculum aromaticum.* [6] Schizocarp of *Petroselinum sativum.* [7] Schizocarp of *Carum carvi.* All the figs. enlarged. (After Baillon.)

Types of Fruit.—When the seed-case derived from the pistil becomes altogether fleshy and succulent, the fruit is termed a *Berry.* From inferior pistils arise inferior berries. From superior pistils superior berries. The berries of the Bitter-sweet (*Solanum Dulcamara*), of the Deadly Nightshade (*Atropa Belladonna*), of the Barberry (*Berberis vulgaris*), and of the Vine (*Vitis vinifera*) are superior; those of the Mistletoe (*Viscum album*), and of the Gooseberry (*Ribes Grossularia*) are inferior. The berry of the Mezereon (*Daphne Mezereum*) is also superior, but is peculiar in that the flesh is contributed not only by the pericarp proper (fruit-wall), but also by the outmost layer of the seed-coat. It is the inner layer of the seed-coat which here gives rise to the stone.

When the outer part of the pericarp is fleshy, and the inner part which immediately invests the seeds stony, the fruit is called a *Drupe* or stone-fruit. The majority of drupes, *e.g.* the Sloe (*Prunus spinosa*), and Cherry (*Prunus avium*), contain only a single stone and seed. That of the Buckthorn (*Rhamnus*) contains two stones, each of which contains a seed, whilst that of the Elder (*Sambucus nigra*), usually described as a berry, is in reality a drupe containing from 2–4 stones each with one seed.

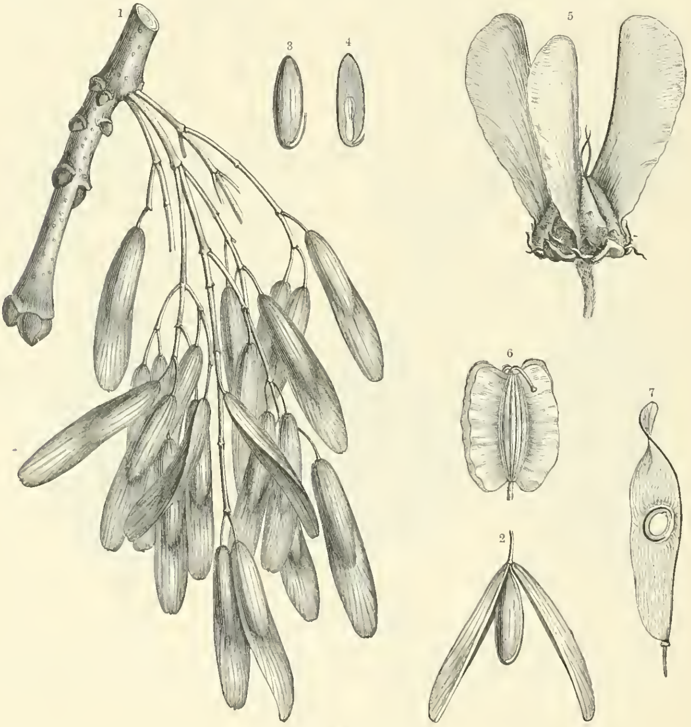

Fig. 323.—Winged Fruits.

1 Cluster of fruits of the Ash (*Fraxinus excelsior*). 2 A single fruit artificially opened. 3 Seed of *Fraxinus excelsior*. 4 The same seed in longitudinal section. 5 Fruit of *Banisteria*. 6 Fruit of *Angelica sylvestris*. 7 Fruit of *Ailanthus glanaulosa*, the central, seed-containing portion seen in section. (Partly after Baillon.)

In a very large number of fruits the pericarp is entirely dry. These *dry* fruits may be distinguished into *Indehiscent fruits*, *Schizocarps*, and dry *Dehiscent fruits*. The indehiscent fruit never opens spontaneously. When ripe it comes away with the inclosed seed and is concerned in the dispersal and establishment of this seed. The indehiscent fruit is termed a *Nut* when it arises from a pistil constituted of more than one carpel, as in the Lime (*Tilia*, figs. 321 2 and 321 3), an *Achene* when produced from a monocarpellary pistil. When the contained seed is entirely fused with the lining of the fruit-wall, as in Grasses (*cf.* vol. i. p. 599, fig. 141 3), the fruit is termed a *Caryopsis*. Sometimes the wall of the nut consists of an outer more fleshy layer, and an inner harder layer after the manner of a drupe. Such a fruit, as in the Fumitory (*Fumaria*, figs. 322 1 and 322 2), is known as a drupaceous nut. As a rule the nut is uni-loculate and contains but a single seed; and this notwithstanding the terms of our definition, according to which a nut is the product of a multi-carpellary ovary. Actually in development all the chambers but one (which contains the ripe seed) atrophy. Only rarely are nuts multilocular, as in the Water-star (*Callitriche*, figs. 322 3 and 322 4) which has a 4-chambered nut and forms a transition to the schizocarp.

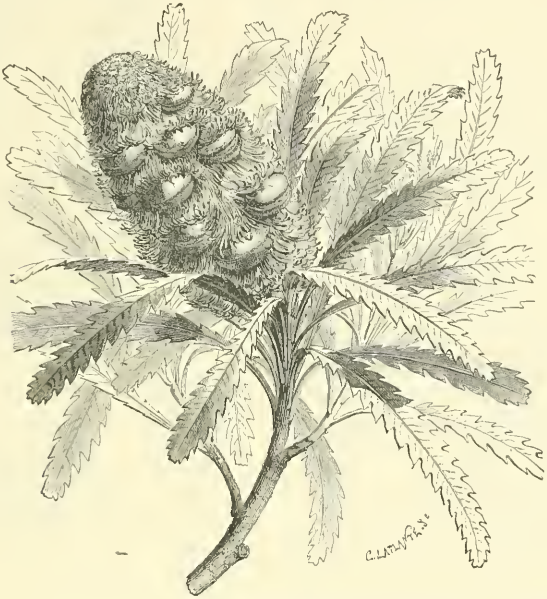

Fig. 324.—Flowering branch of *Banksia serrata* with thick-walled dehiscent capsules. (After Baillon.)

The *Schizocarp* may be regarded as consisting of a number of Achenes united together. Two or more carpels, each containing a seed, remain joined together during ripening, and only later, when the seed is ripe, do they separate from one another, as though the original fruit had been cut into its component parts by a sharp knife. Each of these components (known as *Mericarps*) remains indehiscent like an achene, and is distributed with its contained seed. As a type of these schizocarps the Mallow (*Malva*) may be taken. In the Umbelliferæ the two mericarps into which the schizocarp splits remain for a long time suspended from the tips of a forked prolongation of the axis, as in the fruits of the Caroway (*Carum carvi*, fig. 322 [7]), Parsley (*Petroselinum*, fig. 322 [6]), and Fennel (*Fœniculum*, fig. 322 [5]).

As already mentioned, the pericarp of many indehiscent fruits assists in the dispersal and establishment of the inclosed seeds. This may happen in two ways. The surface of the fruit may bear hairs, curved bristles, or hooked spines which become attached to the coats of animals; or wings, plumes, &c. may be produced, allowing the fruit to be readily borne away even by the gentlest of breezes. Such winged fruits are termed *Samaras*, and many forms of them are distinguished by the descriptive botanist. To these remarkable fruits, however, we shall return in detail later on when dealing with the dispersal of plants; it will suffice here to indicate briefly a few forms. The fruits of the Ash (*Fraxinus excelsior*) are shown in figs. 323 [1, 2, 3, 4]). The pericarp of each consists actually of two carpels joined together; it is continued into a well-marked membraneous wing. Fig. 323 [7] represents the samara of the Tree of Heaven (*Ailanthus glandulosa*) which is continued below and above the seed-containing portion into a thin, spirally-twisted wing. In the fruit of the Umbelliferous *Angelica sylvestris* (fig. 323 [6]) each half (mericarp) shows a sinuous wing-like fringe on either side, whilst in *Banisteria* (fig. 323 [5]) there projects from the back of each component a membraneous continuation resembling a butterfly's wing.

Dry dehiscent fruits are also known as *Capsules*. When ripe their pericarp, which is quite dry, opens and liberates the seeds in a variety of ways. The empty capsule remains, as a rule, on the parent plant, or comes away in pieces (*valves*) at the time of dehiscence. In neither case, however, has the pericarp any further concern with the seeds after these are once liberated. These capsules are the commonest class of fruit, and as their structure is characteristic of many genera, their various modifications have received distinctive names. When the pericarp arises from a single carpel, and at ripening opens along one side, along the so-called *ventral suture*, whilst the opposite side (the *dorsal suture*) is unsplit, or but partially, one speaks of the fruit as a *Follicle*. As a rule several follicles are collected together in a cluster at the end of the flower-stalk, as, for instance, in Monkshood (*Aconitum*) and in the Star Anise (*Illicium anisatum*, *cf.* fig. 325 [1]); more rarely are they solitary, as in certain species of Larkspur (*Delphinium*). In the Proteaceæ, also, a single follicle arises from each flower, and in the Australian "Wooden Pear" (*Xylomelum pyriforme*, fig. 325 [2]), belonging to this order, the huge and extraordinarily thickened follicle splits completely down the ventral and halfway down the dorsal suture. In *Banksia*, also, of which a head with fruits is shown in fig. 324, the follicles are very hard and woody.

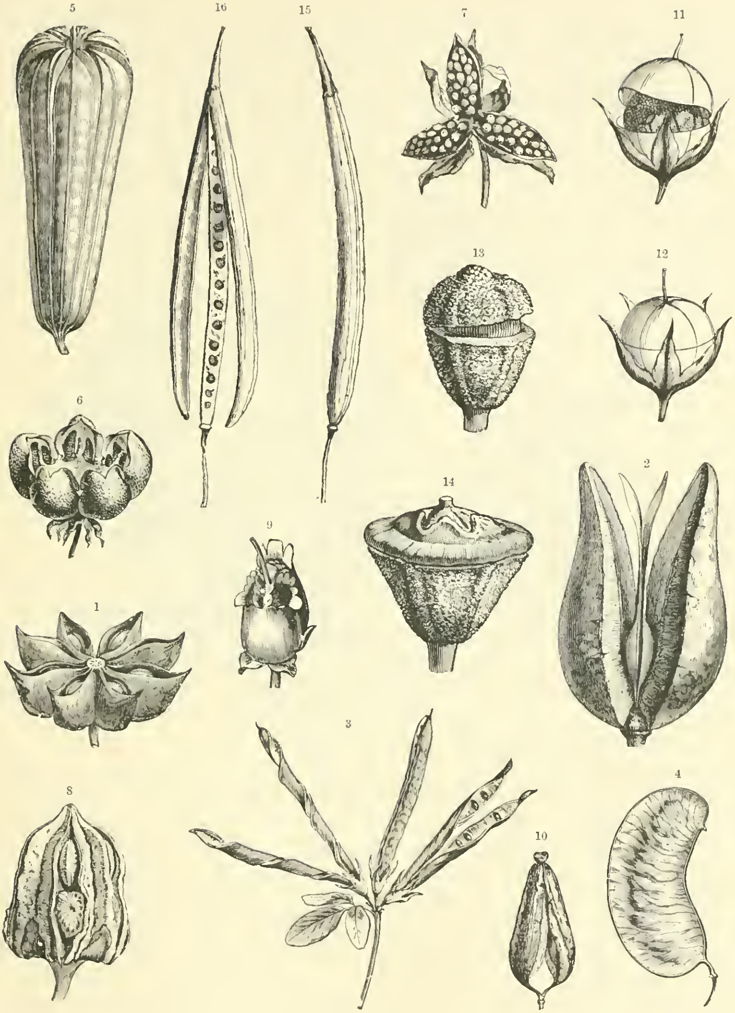

Fig. 325.—Various Capsular Fruits.

1 Follicles of *Illicium anisatum.* 2 Follicle of *Xylomelum pyriforme.* 3 Pods of *Lotus corniculatus.* 4 Pod of *Cassia angustifolia.* 5 Capsule of *Aristolochia.* 6 Capsule of *Ruta.* 7 Capsule of *Viola.* 8 Capsule of *Oxalis.* 9 Capsule of *Antirrhinum.* 10 Capsule of *Cinchona.* 11, 12 Capsules of *Anagallis.* 13, 14 Capsules of *Eucalyptus.* 15, 16 Siliquas of *Brassica.* 5, 10, 11 enlarged; the rest natural size. (After Baillon.)

Like the follicle, the *Legume* or *Pod* arises from a single carpel, but on ripening it splits down *both* sutures completely to the base into two valves, which at the moment of dehiscence become rolled up spirally. This type of fruit is extremely common in the Leguminosæ. As examples may be mentioned *Lotus corniculatus* (fig. 325 [3]) and the Senna (*Cassia angustifolia*, fig. 325 [4]).

Dry dehiscent fruits, the product of two or more carpels, are termed *capsules* in the restricted sense. We may distinguish several types of capsules; (1) such as split into valves from the apex, as in the Birthwort (*Aristolochia*, fig. 325 [5]), Rue (*Ruta*, fig. 325 [6]) and Violet (*Viola*, fig. 325 [7]); (2) such as open by means of teeth restricted to the apex, as in Caryophyllaceæ; (3) such as split longitudinally down the side-walls, the actual cavities of the fruit opening, as in the Wood Sorrel (*Oxalis*, fig. 325 [8]); (4) such as produce several large apertures by the folding back of teeth, as in the Snapdragon (*Antirrhinum*, fig. 325 [9]); and (5) such as form numerous small pores by the shrivelling of restricted areas, as in the Poppy (*Papaver*). The capsules of the Cinchona-tree (*Cinchona*, fig. 325 [10]) split into two valves, which remain attached at the apex, separating at the base only; whilst many capsules dehisce transversely, a lid being removed, as in the Pimpernel (*Anagallis*, figs. 325 [11] and 325 [12]) and *Eucalyptus* (figs. 325 [13] and 325 [14]).

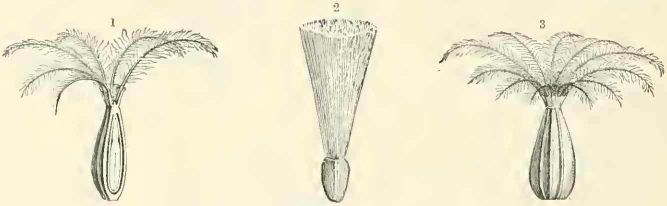

Fig. 326.—Achenes provided with a plume or pappus.

[1] Fruit of Valerian (*Valeriana officinalis*). [2] The same in longitudinal section. [3] Fruit of the Artichoke (*Cynara Scolymus*). (After Baillon.)

A special form of capsule, known as the *Siliqua*, is characteristic of most Crucifers. It is usually described as consisting of two carpels, the exposed walls of which come away, leaving a framework (the *replum*) to which the seeds are attached. Stretched upon this framework is the membrane which formed the ("false") partition of the ovary. This class of fruit is well shown in Honesty (*Lunaria*) and in the Cabbage (*Brassica oleracea*, figs. 325 [15] and 325 [16]). According to the terminology given at p. 75 (4), the two valves which come away correspond to the two outer non-ovule-bearing carpels, whilst the ribs which remain are the two inner ovuliferous carpels.

Though, in a great number of Angiosperms, the various floral-leaves disarticulate and fall away after pollination and fertilization, this is not universally the case; in a considerable number some of them remain behind, undergo various changes, and form an outside investment or appendage to the fruit which plays an important part in the dispersal or preservation of the seeds. The same is true of the bracts and bracteoles, the leafy structures which are present in the immediate vicinity of the flowers, though not actually included in them. We may distinguish, perhaps, amongst these accessory structures of the fruit, between such as arise from portions of the perianth on the one hand, and such as are formed from bracts and bracteoles on the other. The enumeration of these structures here, however, must be distinctly limited to a few of the more commonly occurring.

A curious form of fruit obtains in the Mulberry (*Morus*). The female flowers in this tree are arranged in little catkin-like clusters. Each flower consists of an ovary inclosed in an inconspicuous four-leaved perianth. From each ovary a tiny nut arises; but the ripe fruit resembles a succulent berry rather than a collection of nuts. This is due to the fact that after fertilization, whilst the ovaries are developing into nuts, their perianths become distended and fleshy, altogether concealing the ovaries. Without a knowledge of the mode of development, the perianth might now be readily mistaken for the true fruit-wall (pericarp), and the nut for the seed In several species of Trefoil (e.g. *Trifolium agrarium, badium, spadiceum*) the papilionaceous corolla is yellow. After fertilization this turns brown, dries up and forms a flying-arrangement for the small fruit within (*cf.* figs. 442 [1, 2, 3, 4, 5]).

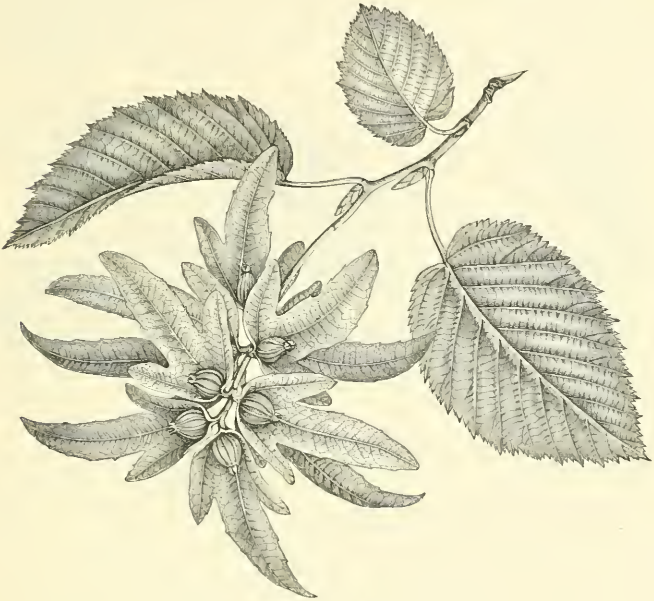

Fig. 327.—The Hornbeam (*Carpinus Betulus*) in fruit.

It very frequently happens that the *Calyx* is retained as an accessory to the fruit. In the Winter Cherry (*Physalis Alkekengi*), a solanaceous plant often cultivated in gardens, the calyx, originally small and green, becomes much inflated during ripening and forms a bright red bladder inclosing the actual berry; in the Henbane (*Hyoscyamus*), belonging to the same family, the calyx tightly incloses the capsular fruit, its periphery forming a characteristic funnel around the top. In Labiatæ the calyx persists as a short tube, or as a bell or pitcher, at the base of which the actual fruit is found. In the Water Chestnut (*Trapa natans*, *cf.* vol. i. p. 607, fig. 144^{3}) the four segments of the calyx become hardened and persist as four spines arranged cross-wise around the fruit. In many Valerians, Composites, and Scabiouses, the calyx persists, growing, as the fruit ripens, into a radiating crown of bristles or feathery hairs. This crown, known as a *Pappus*, serves the achene as a parachute (*cf.* figs. 326$^{1, 2, 3}$ and fig. 447).

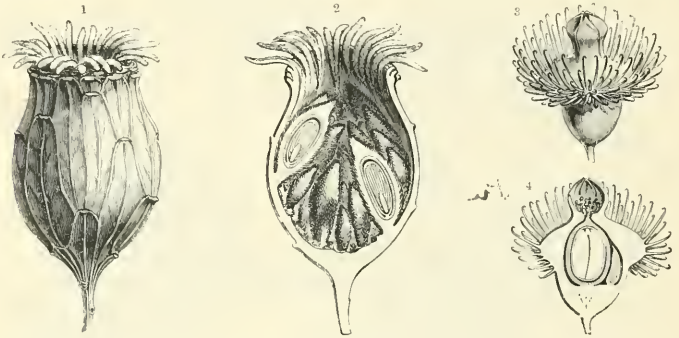

Fig. 328.—Fruits with persistent receptacles.

^{1} The Carolina Allspice (*Calycanthus*). ^{2} Longitudinal section of the same. ^{3} Fruit of *Agrimonia*. ^{4} Longitudinal section of the same. (After Baillon.)

Amongst the Amentaceæ, trees whose flowers are for the most part destitute of perianth, the *bracts* and *bract-like scales* associated with the flowers often play a prominent part in the fruit. In the Grasses also the same feature is noticeable. In these latter the actual grain is very frequently closely enwrapped by one of the glumes, so tightly indeed, that they easily escape observation, as in Barley, Oats, and many others. The greatest variety of fruit-investment is met with in the Cupuliferæ and allied Amentaceæ, which include the Hornbeam, Hop-hornbeam, Beech, Hazel, and several other well-known trees. The actual fruit in all these is a nut, but inclosed in a peculiar involucre-like sheath (the *cupule*) derived from bract-like scales external to the flowers. In the Oak (*Quercus*) the cupule is cup-like (figs. 329^{1} and 329^{2}); in the Beech (*Fagus*) it completely envelops the paired triangular nuts, and is spiny outside, at ripening it bursts into four valves like a capsule; in the Chestnut (*Castanea*) it is extremely prickly, and, as in the Beech, bursts into valves (fig. 339^{4}); in the Hazel (*Corylus*) it forms a laciniated, leathery envelope to the nuts (fig. 235, p. 147), whilst in the Hornbeam (*Carpinus*, fig. 327) it has the form of a three-lobed open scale, to the base of which the ribbed nut is attached. Finally, in the Hop-hornbeam (*Ostrya*, fig. 437 [6]) it forms a loose papery envelope.

The *Receptacle* of the flower is not infrequently a conspicuous feature in connection with the fruit. This is well shown in the Carolina Allspice, in Roses, and in Pomaceæ. In the Carolina Allspice (*Calycanthus*, figs. 328 [1] and 328 [2]) an excavated pitcher-like receptacle, invested on the outside with scales, incloses the achenes; in the Rose there is a similar inclosure, here smooth and fleshy, and bearing a five-leaved calyx above, this constitutes the hip. In the Apple, Pear, Quince, and other Pomaceæ, the receptacle forms an extremely succulent mass, in which the actual fruit is imbedded, and with which it is entirely fused (*e.g.* Quince, *Cydonia*, fig. 330 [2]). In the Strawberry (*Fragaria*), on the other hand, the fleshy receptacle is convex, and bears the little achenes scattered over its surface. Not always, however, is the receptacle fleshy; thus, in the Agrimony (*Agrimonia Eupatoria*, figs. 328 [3] and 328 [4]) it forms a dry and woody inclosure for the one or two achenes, and is provided with numerous stiff hooked bristles on its periphery.

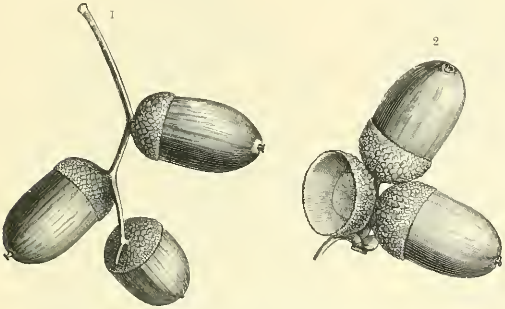

Fig. 329.—Fruits with Cupules

1 *Quercus pedunculata.* 2 *Quercus sessiliflora.*

Much less frequently does the *flower-stalk* (pedicel) take a share in the fruit formation. This is so, however, in Anacardiaceæ, in some Rhamnaceæ, and in a few other groups. Thus, for instance, in the tree which produces Cashew-nuts (*Anacardium occidentale*, fig. 330 [1]), the upper portion of the pedicel swells up into a fleshy pear-like structure; on its summit is perched the kidney-shaped nut with its inclosed seed. In *Hovenia dulcis* (allied to the Buckthorn) a similar arrangement prevails, the flower-stalks are swollen, and contain a sweet red pulp appreciated by the Chinese and Japanese. To these instances may be added the Fig (*Ficus*, *cf.* figs. 240 [10] and 240 [11], p. 157), in which the whole receptacle of the inflorescence is excavated, urn-wise, and becomes very succulent on ripening. The little grains inside, commonly taken for seeds, are in reality the actual fruits or nuts, each of which contains a seed. As a final instance may be mentioned the polygonaceous *Brunnichia africana* from west tropical Africa; in this case the flower-stalk becomes winged down either side, from its point of insertion up to the nut at its apex. It thus serves as a distributing organ for the fruit.

In many plants whose flowers are clustered very close together it often happens that the fruits of the several flowers as they increase in size become more or less fused together; or the axis which bears them, or other associated parts, become fleshy forming a succulent matrix for the individual fruits. Such a mass of fruits is termed a *collective fruit.* Good examples of this are the Mulberry (*Morus*), the Pine-apple *Ananassa sativa*), Piperaceæ, *e.g.* Betel Pepper (*Piper Betle*, fig. 331^{1}); and Artocarpeæ, *e.g.* the Bread-fruit (*Artocarpus incisa*, fig. 332) and Jack-fruit (*Artocarpus integrifolia*). With these collective fruits may be contrasted the clustered crowded carpels produced from *single flowers* (*aggregate fruits*), such as the Raspberry (*Rubus Idæus*), *Calycanthus*, Rose, &c., already described, also many Anonaceæ, as, for instance, the West-Indian Sour-sop (*Anona muricata*, fig. 331^{4}), the Sweet-sop (*Anona squamosa*, figs. 331^{2} and 331^{3}) and Custard-apple (*Anona reticulata*). The terminology that has grown up around the types of fruit described in this paragraph is extremely confusing and slovenly. We propose to call the compound fruit arising from a number of crowded flowers a *collective fruit*, that from the carpels of a single flower an *aggregate fruit.* An altogether peculiar fruit is that of the Lotus Lily (*Nelumbium speciosum*, *cf.* figs. 333 and 334). Here the receptacle is enlarged into a huge top-shaped structure in the middle of the flower (fig. 334^{1}); the upper surface of this top is like a honey-comb, and in each "cell", a carpel is sunk as in a socket

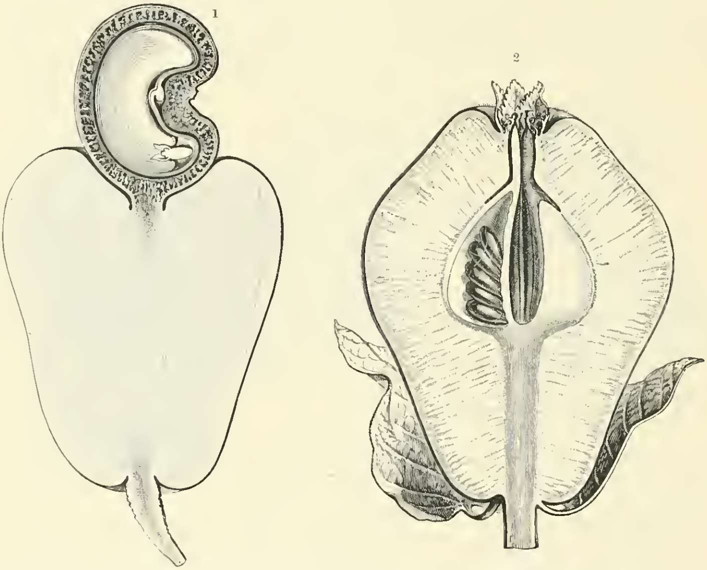

Fig. 330.—Fruits in whose structure the receptacle and pedicel take a share.

1 Longitudinal section of the fruit of the Cashew-nut Tree (*Anacardium occidentale*). 2 Longitudinal section through a Quince (*Cydonia*). (After Baillon.)

(fig. 334 ²). When the fruit is ripe and dry, these carpels form hard, woody achenes which rattle in their loose sockets like teeth in the jawbone of a skull.

Our descriptions of the fruit and its various forms and modifications relate, so far, solely to the Angiosperms. In the *Gymnosperms*, however, several essential differences are to be noted. The account of their methods of fertilization (pp. 418–420) was left at that stage at which the male sexual cell had fused with the egg-cell. The nucleus of the fertilized egg now moves down to the base (away from the micropyle) of the egg-cell and divides several times, each product of its division becoming enveloped in protoplasm and ultimately in a cell-wall. In the Gnetaceæ which many Botanists regard as more nearly allied to the Angiosperms than either of the other two families of Gymnosperms (Coniferæ and Cycadaceæ), there arise in this way from 2–8 daughter-nuclei around each of which protoplasm aggregates, and a cell-membrane is formed (*cf.* fig. 315 ², p. 415). Between each of these cells there is no connection: each grows out into a tube which penetrates the wall of the egg-cell and pushes its way down into the reserve-food (endosperm) below. From the tip of the tube a small cell, the embryonal cell, is cut off and from this cell by further division and growth an embryo is produced, which is nourished by the food-material. Of the many embryos which are inaugurated, one only comes to maturity, and is found in the ripe seed.

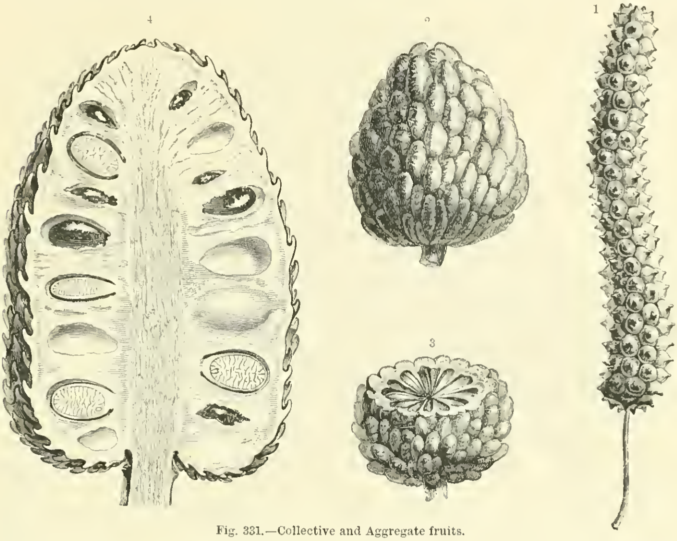

Fig. 331.—Collective and Aggregate fruits.

¹ Collective fruit of Betel Pepper (*Piper Betle*). ² Aggregate fruit of Sweet-sop (*Anona squamosa*) formed by fusion of the carpels of a single flower. ³ Transverse section of the same. ⁴ Longitudinal section of the aggregate fruit of the Sour-sop (*Anona muricata*) produced in the same way. (After Baillon.)

In the Silver Fir, Spruce Fir, Pine, and other Conifers, comprised under the family Abietineæ, the nucleus of the egg-cell divides into four at the base of the egg-cell, and here four little cells are produced, arranged like a rosette at that end. Each of these is divided into three stories, and the four cells forming the middle story elongate, diverge, and grow down into the endosperm, carrying the little embryonal cells at their tips. The four cells of the upper story remain attached to the residue of the egg-cell, and serve as a fulcrum for the elongating tubes—the suspensors. As in the Gnetaceæ, the embryonal cells become modified into embryos, but ultimately only one of them prevails, and, growing at the expense of the food-material, is a conspicuous object in the ripe seed (fig. 335 [6]). A portion of the endosperm remains as a mantle around the embryo, and is only absorbed at germination.

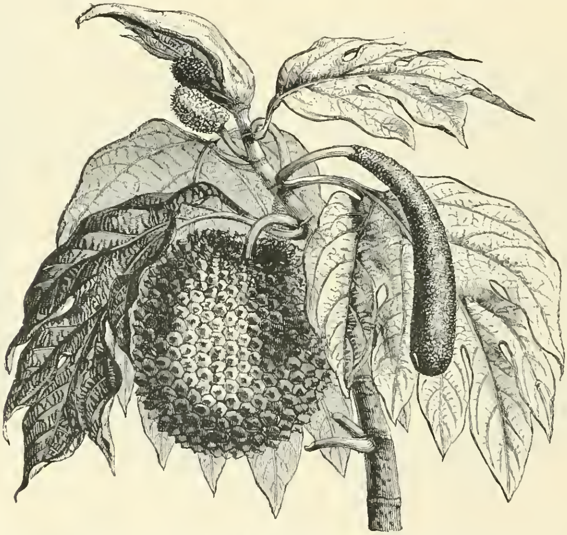

Fig 332.—Branch of the Bread-fruit Tree (*Artocarpus incisa*) showing a male inflorescence (sausage-shaped, to the right), a female inflorescence (globular, near the apex) and a collective fruit (to the left). (After Baillon.)

In the Juniper, Arbor Vitæ (*Thuja*), Cypress, and other Conifers belonging to the family Cupressineæ, each egg-cell, after fertilization, gives rise to but a single embryo (though there are exceptions to this rule). Otherwise the events are not very different from those occurring in the Abietineæ.

The *Integument* of the ovule in Gymnosperms forms the seed-envelope (or testa), as in Angiosperms. The *Micropyle* becomes closed up, and the whole testa very hard. In the Pines, Firs, &c. (Abietineæ), the micropyle points *away from* the free margin of the open scale which bears the ovules (fig. 335 [7]), *i.e.* towards the axis of the cone; in the Cypress and other Cupressineæ, on the other hand, *towards* the free margin of the scale (figs. 337 3, 4, 6), and away from the axis of the cone.

In several species, as in the Stone Pine (*Pinus Pinea*) and the Arolla Pine (*Pinus Cembra*), the seed-coat attains a thickness of 1½ to 2 millimetres, so that the seed resembles a nut in appearance. Both these species, indeed, serve as an article of diet, being eaten like nuts. The seeds of Pines and Fir-trees are provided with a one-sided wing (*cf.* figs. 335 3, 4, 5) which plays an important part in their dispersal by wind. In the Maidenhair Tree (*Gingko biloba*) the integument of the seed becomes succulent and coloured a bright orange, so that the seed in a way resembles a drupe (*cf.* fig. 337 7). In *Cycas revoluta*, also, the integument becomes red and fleshy (*cf.* fig. 208 7, p. 74)

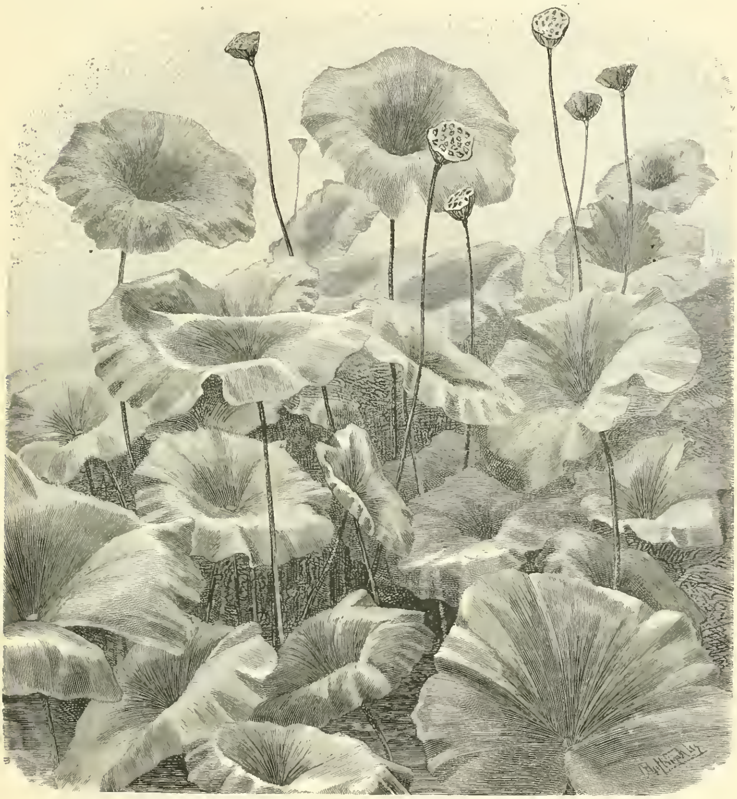

Fig. 333.—The Lotus Lily (*Nelumbium speciosum*). (From a photograph.)

The ovules of both Abietineæ and Cupressineæ are inserted upon scales of varying form, the insertion of which on the axis of the cone may be broad or narrow (*cf.* figs. $335^{7, 8, 9}$ and $337^{3, 4, 6}$). These scales form an important constituent of the ripe cone, and are known as the *ovuliferous scales.* In not a few cases, as in the Silver Fir (*Abies pectinata,* figs. $335^{1, 2, 3, 4}$) and Larch (*Larix,* figs. 335^{8} and 337^{1}), there exists a second scale, the *bract scale,* beneath each ovuliferous scale, and subtending the same. In the Pine, also, both scales are present, though in the ripe cone there are no signs of the bract-scales at the exterior owing to the fact that they become entirely overgrown and embedded between the big ovuliferous scales.

In the Abietineæ the scales of the cones are inserted in a continuous spiral (*cf.* fig. 335^{1}, and vol. i. p. 403, fig. 101), whilst in Cupressineæ the scales are inserted in whorls of 2 or 3 scales each (*cf.* figs. $336^{6, 7}$ and $337^{3, 5}$). In both, the margins of the scales overlap, and the seeds are ripened in the slit-like chinks between them (*cf.* 336^{6} and 337^{5}). The whole assemblage of scales constitutes an aggregate fruit, and is known as a *cone.* The scales may be hard and woody, when we have a woody cone (335^{1} and $337^{1, 2, 5}$); or they may be succulent, giving a fleshy cone. In such fleshy cones very few of the whorls are succulent, the central axis is very short, and the whole structure has much the appearance of a berry, as in the Juniper (*Juniperus communis,* figs. 336^{7} and 336^{8}).

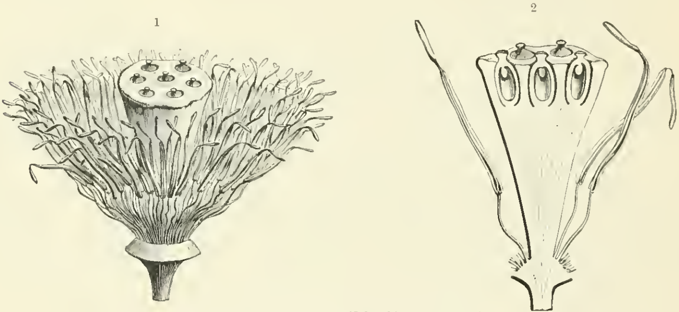

Fig. 334.—The Lotus Lily (*Nelumbium speciosum*).

1 Flower from which the perianth-leaves have been removed; expanded receptacle in centre. 2 Longitudinal section through the top-shaped enlargement of the receptacle, showing three carpels embedded in their sockets. (After Baillon.)

The section of Gymnosperms known as the Taxineæ do not produce cones. Their seeds arise alone or in pairs at the ends of special short branches, or upon the surface of small fruit-scales. The plum-like seeds of the Maidenhair Tree (*Gingko biloba*) are arranged in pairs at the ends of axes which resemble cherry-stalks (see fig. 337^{7}). The seeds of the Yew (*Taxus baccata*) occur at the tips of little scale-bearing shoots, and when ripe are almost completely enveloped in a sweet, fleshy, crimson tissue (see figs. $336^{1, 4, 5}$). This fleshy inclosure, which arises as a circular cushion from the place of insertion of the ovule, is not of the nature of a carpel, it is an aril. In *Podocarpus*, also, is developed a peculiar structure of the same kind.

In Cycads the seeds are borne upon carpels arranged in cones, and have a woody integument. In some cases they correspond in position to metamorphosed lobes of a carpel (*cf.* fig. 208 [7], p. 74), and have the outer layer of their integument developed as a succulent coat. In the Gnetaceæ, the seed at maturity is inclosed in a fleshy "perianth" in *Ephedra*; in *Welwitschia* cone-like collective fruits are produced; finally, in *Gnetum* leaf-structures around the seed unite to form cup-like receptacles for the seeds.

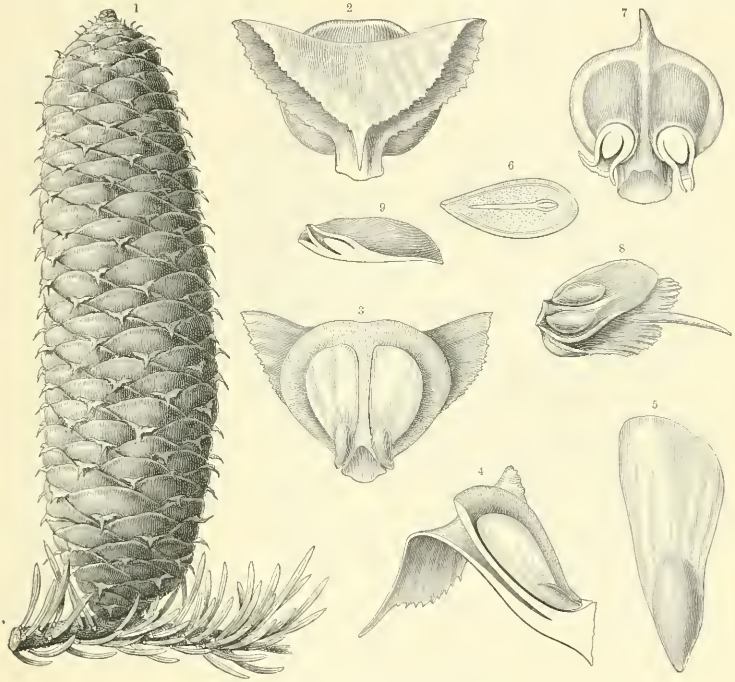

Fig. 335.—Fruit and Seed of Coniferæ.

[1] Cone of the Silver Fir (*Abies pectinata*). [2] Bract scale and ovuliferous scale of the same seen from the outside (the bract scale is pointed). [3] Ovuliferous scale of same seen from above, showing the two winged seeds, and the bract scale behind. [4] Longitudinal section of bract and ovuliferous scales, showing a seed inserted upon the latter. [5] A winged seed of the same. [6] Longitudinal section of the seed. [7] Ovuliferous scale of the Scotch Pine (*Pinus sylvestris*) seen from above; it bears two ovules. [8] Single ovuliferous scale of Larch (*Larix europæa*) showing two ovules on its surface and bract scale (with bristle) below it. [9] Longitudinal section of the ovuliferous scale of the Larch. [1] nat. size; the other figs enlarged.

From the brief observations on the manner of fructification of Gymnosperms, it will be seen that their methods are very various, and that, in all cases, they differ from those of Angiosperms. They agree in the common object of producing a vigorous embryo, and in providing it with adequate safeguards against unfavourable external conditions, and with means of dispersal, when the time comes for the seed to be detached from the parent plant and to take up an independent existence.

Whilst still attached to the parent plant, the embryo needs *protection* against the *ravages* of *animals*, and against *unfavourable climatic conditions.* Means of protection against the former are provided sometimes on the seed-coat, in other cases on the wall of the ovary; or they may be on other structures associated with the flower, or upon the flowering axis itself. These defensive arrangements fall into several groups. First of all, there are thorns, prickles, and spinous bristles, met with especially on the ovary and immediate envelopes of the fruit. The capsule of the Thorn-apple (*Datura Stramonium*), that of the Anatto (*Bixa Orellana*, see fig. 338), the long 3-valved fruits of *Schrankia* (see fig. 339^{2}), the pods of the Russian Liquorice Plant (*Glycyrrhiza echinata*), the persistent calyx of a steppe-plant, *Arnebia cornuta*, and the cupule of the Chestnut (*Castanea vulgaris*, see fig. 339^{4}) may serve as examples. Several Pines, of which the North American *Pinus serotina* is a type, have cones the scales of which are produced into sharp spines (see fig. 337^{2}), so that the seeds are inaccessible to animals till such time as the scales separate and the winged seeds are committed to the wind. Of interest in this connection are certain Crucifers (*Tetractium quadricorne, Matthiola bicornis, M. tricuspidata*, fig. 339^{3}) in which, at the end of the fruit just below the scar of the style, 2, 3, or 4 stiff spines are formed, which make these fruits unaccept-

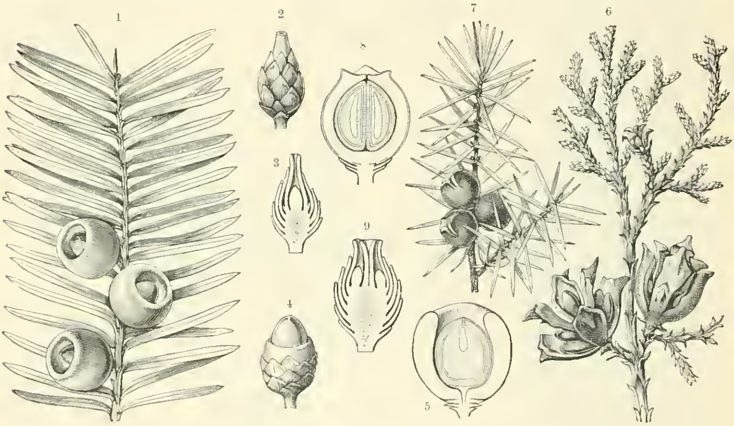

Fig. 336.—Fruits and Seeds of Coniferæ.

^{1} Branch of Yew (*Taxus baccata*) with ripe seeds, each inclosed in its aril. ^{2} Tip of ovule of same projecting from between the scales of the little fertile shoot. ^{3} Longitudinal section of the same. ^{4} Young seed of the same only partly inclosed in its aril. ^{5} Longitudinal section of the ripe seed of the same, showing the aril. ^{6} Branch of the Arbor Vitæ (*Thuja orientalis*) showing female flowers and ripe, burst cones. ^{7} Branch of Juniper (*Juniperus communis*) showing berry-like cones. ^{8} Longitudinal section of one of these cones. ^{9} Female flower of Juniper. $^{1, 6,}$ and ^{7} nat. size; the other figs. enlarged.

able morsels for animals. A less common condition, and one deserving of special mention, occurs in several Mimosas belonging to the immediate alliance of the Sensitive Plant (e.g. *Mimosa pudica, M. polycarpa, M. hispidula*); of these the last-named may serve as type (see fig. 339[1]). The pods here are densely crowded together, and their dorsal and ventral sutures form a strong framework bearing a double row of short spines. These spines hinder all animals from interfering with the fruits. As the seeds ripen, the valves fall away from their spiny framework, and are, with their contained seeds, dispersed by the wind. As a rule, the valves break up at this time into one-seeded segments (fig. 339[1]), and being very light in proportion to their area, are carried considerable distances.

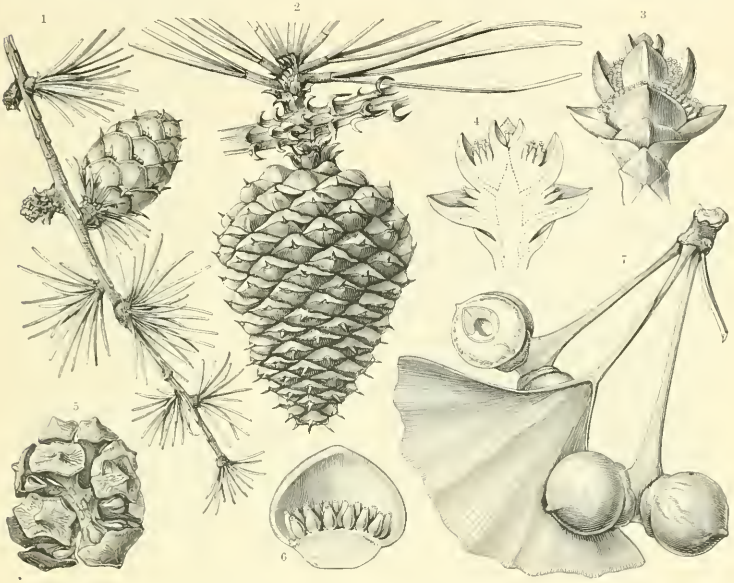

Fig 337.—Coniferous Fruits and Seeds.

[1] Branch of the Larch (*Larix Europæa*) with ripe cone. [2] Branch of *Pinus serotina* with ripe cone. [3] Female flower of the Cypress. [4] Longitudinal section of the same. [5] Ripe cone of the Cypress (*Cupressus sempervirens*). [6] Single carpel of the Cypress with numerous ovules. [7] Branch of *Gingko biloba* with unripe fruit. [1, 2, 5, 7] natural size. The other figures enlarged.

In the instances just enumerated the protection is provided only up to the time that the seeds are ripe. With the severance of the seeds from the parent plant the protective function of the spines is at an end. The spinose investment as a rule remains upon the plant, and only rarely, as in the winged fruit of *Centrolobium robustum* (see fig. 339[5]), does the thorny ovary wall (pericarp) become detached with its contained seed. Under these circumstances the spines may play a further part, either by serving as a mechanism of dispersal, or by fixing the seed in the germinating bed.

In the case of plants with succulent fleshy fruits, the seeds of which are distributed by birds, it would be extremely disadvantageous for the fruits to be provided with spines or prickles when ripe. In point of fact, when such structures are present they often disarticulate and fall away as the fruits ripen, so that birds may have unhindered access to them. The fruits of the leguminous *Mucuna pruriens* are clad during their ripening period with a felt-work of serrated bristles, which contain an irritating fluid. These bristles cause an intolerable itching, or even an eruption of the skin, and, so long as they remain on the fruit, effectively guard it from animals. But as the seeds ripen, and the fruit becomes pulpy, these bristles fall away (so it is stated), and animals are no longer repulsed, but devour the pulp, and so disperse the seeds.

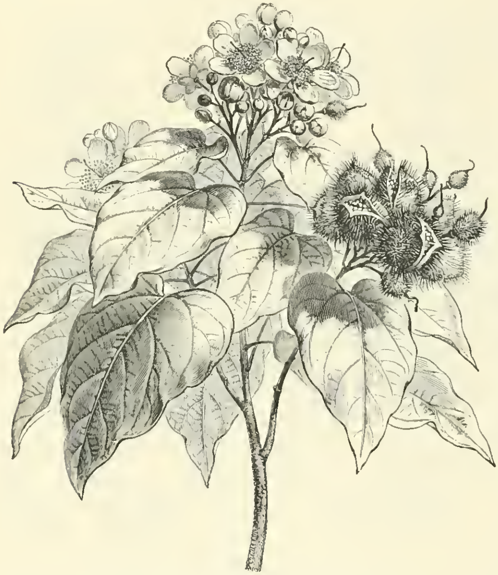

Fig. 338.—Protection of ripening seeds against animals.

The Anatto plant (*Bixa Orellana*) with flowers and fruit. Three of the fruits have opened showing the seeds. (After Baillon.)

The well-known Hips of Roses which ripen in the autumn, do not fall away from the plant, but remain attached. The seeds are contained in hard and tiny nut-like fruits, which are inclosed in the fleshy and excavated receptacle. They are destined to be distributed by blackbirds, jackdaws, and other birds, which devour the hips for the nutriment contained in the fleshy investment; the little nuts, however, pass out undigested in the droppings in some place more or less distant from the Rose-bush. Whilst these birds, attracted by the coloured fruits, are welcome guests, the case is quite the reverse as regards mice and other little rodents; they gnaw the nuts, and devour their contents, the seeds. But the Rose-hips are well-protected against these animals. The stems and branches, up which they must climb to reach the fruits, are provided with sharp prickles with downwardly-directed points, which give complete immunity against these animals. I have repeatedly, in the late autumn, when the mice desert the fields and take up their winter-quarters in the abode of man, strewed the ground in my garden with Rose-hips of an evening. Invariably, next morning, I found that they had been gnawed and demolished by mice, whilst those remaining *in situ* on the plants were untouched. The fruits of several dwarf Palms are similarly defended against the attacks of animals, by zones of spines upon the stem, prickles upon the floral investments, &c. The berries of several shrubby Solanaceæ (e.g. *Solanum sodomæum*, and *S. sisymbriifolium*) gain a like protection, as do those of the Blackberry, from numerous prickles which clothe the stem and even the fruit-stalk and calyx. In several members of the Gorse genus, *Ulex Gallii*, *micranthus*, and *nanus*, the pods are borne upon branches which bristle with spines. The spines project beyond the pods, and their sharp points being directed downwards, mice are prevented from climbing up and working havoc.

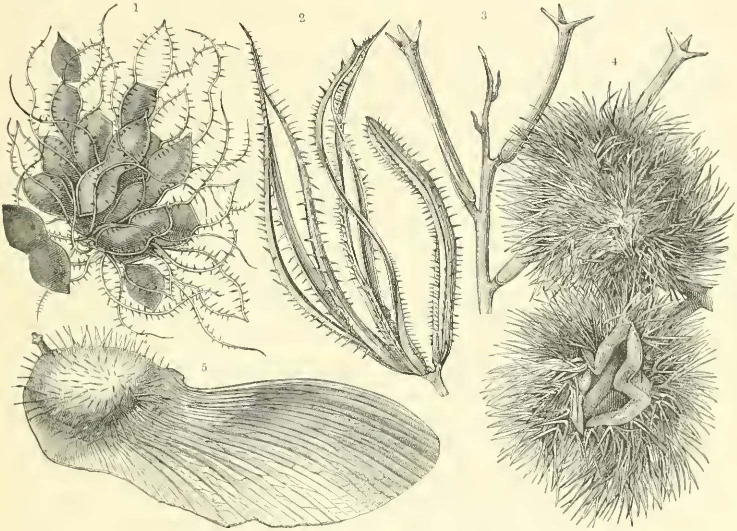

Fig. 339.—Protection of ripening seeds against the attack of animals.

[1] *Mimosa hispidula.* [2] *Schrankia.* [3] *Matthiola tricuspidata.* [4] *Castanea vulgaris.* [5] *Centrolobium robustum.*

Other animals besides these rodents, such as caterpillars, snails, earwigs, centipedes, and the like, have to be warded off. Some caterpillars find the green ovaries acceptable as food, others the seeds themselves. Still, as we have seen, it is of direct advantage to several Caryophyllaceæ, Leguminosæ, and species of *Yucca*, that a portion of the seeds should fall to the lot of insect-larvæ (*cf.* pp. 153-161). It may be repeated here that prickles and spines, the points of which are directed upwards, serve to protect the foliage against browsing animals (*cf.* vol. i. p. 432). In the above-mentioned case of the Gorse, the spines towards the tips of the branches keep browsing animals away, whilst those inserted lower down, which are directed earthwards, prevent mice from climbing up the plant.

A peculiar protective contrivance has been observed on the calyx of several Labiates, *e.g. Thymus, Calamintha, Ballota.* The corolla falls away after fertilization, but the calyx persists, forming a sheathing envelope for the 4 nutlets. For the better protection of these nutlets the mouth of this cup-like envelope is closed by the development of a crown of hairs, which is impenetrable to small, seed-devouring animals. A further use of these envelopes in seed-dispersal will be alluded to in another place.

In other cases fruits are protected against unwelcome guests, not by spiny structures, but by the elongation of their stalks during ripening, rendering them inaccessible. Thus it would be a difficult feat for a mouse to reach the pendent pods of the Pea (*Pisum*), or those of the Vetches (*Vicia dumetorum, V. pisiformis, V. sylvatica*). Should by any chance a pod be accessible to these animals, by some other route, it is as good as lost, as the nutritious seeds of these plants are much sought after by them. Cherries also, on their long stalks, no doubt derive considerable immunity from earwigs, centipedes, &c., as those which fall to the ground are speedily attacked and devoured.

In the case of seeds whose dispersal depends on the attraction of animals by sweet, fleshy pericarps, these tissues are the reverse of appetizing before they are ripe; not until the seeds are ready to be separated from the parent plant do fruits of this kind become attractive. It is only necessary to cite as instances unripe Cherries, Plums, Apples, and Grapes. It was stated on a previous occasion (vol. i. p. 462), when dealing with chemical changes occurring in plant-tissues, that the fleshy parts of fruits are rendered disagreeable to animals before they are ripe by the presence of bitter or poisonous glucosides, &c. Later on these substances are altered, perhaps under the influence of the acids, which are present in large quantities in unripe fruits, and their place taken by sugars and other harmless materials; thus, what is at first unattractive, and even repulsive, becomes, on ripening, a nutritious food, much sought after by animals, which, at the same time, unconsciously disperse the contained seeds. In this connection the Walnut (*Juglans regia*) is very instructive. Until the seed contained in the "nut" (here really the stone of a drupaceous fruit) is ripe, the latter is surrounded by a fleshy investment rich in tannin. It is not known at this stage that the "nuts" are ever interfered with by nut-crackers or other animals. But on the ripening of the seed the fleshy envelope splits, and the "nut" becomes accessible.

In other cases it is not by acids or bitter stuffs that the seeds are protected, but by strong-scented resinous or sticky substances, which are contained in the cells and passages of the fruit. Thus, in the scales of the cone of the Arolla Pine (*Pinus Cembra*) quantities of resin are present until the seeds are ripe. If the cones be cut with a knife this resin escapes, and can only be removed from the blade with the utmost difficulty. Were a nut-cracker to peck the scales at this stage to obtain the young seeds, its beak would get all besmirched with the resin. It is easy to observe at Zermatt and Arolla in the Pennine Alps, where this Pine grows, that the nut-crackers attack only the fully-ripened side of even almost ripe cones. As the cone ripens the seeds become easily accessible, but with their manner of dispersal we shall deal in a later section of this work. Here we are concerned only with the fact that many ovaries and fruit-envelopes render their contents undesirable to animals by sticky secretions or disagreeable scents. The pods of several Leguminosæ, *e.g.* species of *Adenocarpus* (*A. decorticans*, *A. Hispanicus*, &c.), are invested both on their flat sides and round the edge with short-stalked, sticky, brown glands, which are to be regarded as a protective arrangement for the young pod. The same obtains in the Hemp (*Cannabis sativa*), though here it is not the ovary but the scales immediately about it which are sticky and strongly odorous. So also in the Hop (*Humulus Lupulus*), the fruits are invested in scales bearing glands which play a like part. Even the ubiquitous sparrow leaves the fruits of these two plants alone during the period of ripening.

Of not less importance to the young embryo is protection against *injurious climatic influences.* Among these, undue moisture and dryness are the chief; and it is to be expected that due provision against them should be made on behalf of the young plant whilst it remains on the parent. Seeds contained in berries, drupes, and indehiscent fruits, as well as those which, produced in capsules, are dispersed at the moment of fruit-dehiscence, hardly come under consideration here, as the opportunities for hurt by weather are relatively small. But in the case of dehiscent fruits which open by means of valves, teeth, or pores, and in which the seeds are retained for some time after the opening of the fruit before they are scattered, provision must be made against the entrance of rain into the cavity of the fruit, which might injure the seeds. This class of danger is averted by the fact that the various valves, teeth, &c., which guard the apertures of the fruits, are very hygroscopic and close in humid weather; or, what is equivalent to this, they only open in dry weather, especially under the influence of drying winds. To make this remarkable contrivance intelligible we must briefly describe the arrangements for seed-dispersal obtaining in capsules of the kind. Capsules opening by valves, teeth, &c., are usually inserted on long stalks, or, if sessile, the axis from which they arise possesses considerable length. These stalks are fairly stiff, and oscillating to and fro in gusts of wind the contained seeds are shaken out, usually as the capsule springs back after the blast. In the case, for instance, of the beaker-like capsules of the Nottingham Catchfly (*Silene nutans*, fig. 340 [5]) the seeds cannot fall out of their own accord, the opening being directed upwards; but as soon as the wind sets the long stalk in vibration they are jerked out. For this mode of scattering of the seeds it is essential that the apertures of the fruit should be directed upwards. Indeed, in the great majority of cases of this class, this is their position. In this Catchfly at the time of flowering the flower-stalks are pendent (see figs. 238 and 239, pp. 154 and 155), but, as the fruit ripens, the fruit-stalk becomes erect; the same thing is well shown in the Martagon Lily. On the other hand, when the fruit-stalk bends down after flowering, as in the Bellflower (*Campanula*, fig. 340^{1}) and in the Winter Green (*Pyrola*, fig. 340^{6}), the holes and slits are not formed at the apex of the fruit, which is directed downwards, but at its base, close to the insertion of the stalk. This position of the apertures would render the inside of the capsule liable to wetting from rain, &c., and the contained seeds to injury therefrom, were it not for the fact the openings are closed when this danger threatens. The wall of the capsule is very hygroscopic, and the slits and valves quickly close in damp weather. In fig. 340 several examples of this opening and closing are represented. In the already mentioned capsule of the Catchfly (fig. 340^{5}) the aperture at the summit is guarded by a number of divergent teeth; the same is true in the case of those of various species of Toadflax (e.g. *Linaria Macedonica*, fig. 340^{3}). In *Cerastium macrocarpum* (fig. 340^{4}) the opening is directed laterally, and in the Campion (*Lychnis diurna*, fig. 340^{2}) the capsule is erect with revolute teeth. In the Bellflower (e.g. *Campanula rapunculoides*, fig. 340^{1}) small, circumscribed portions of the wall near the base fold back as valves, giving rise to as many apertures; in the Winter Greens (e.g. *Pyrola chlorantha*, fig. 340^{6}) a number

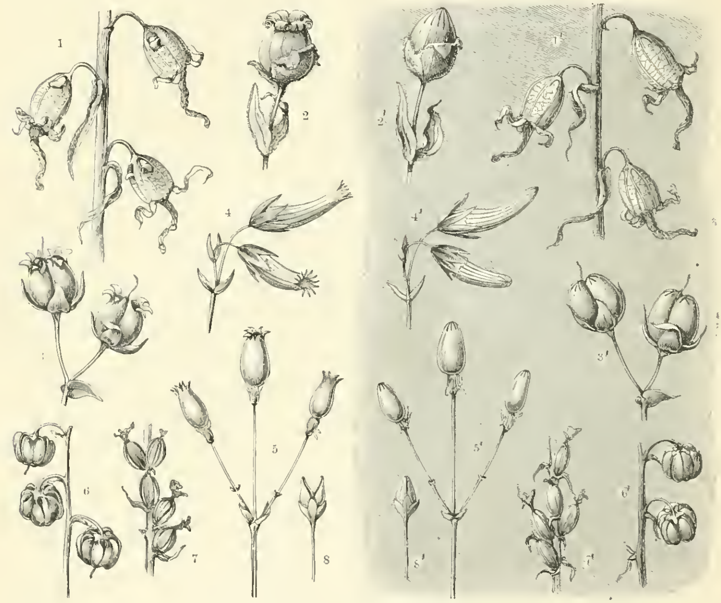

Fig. 340.—Protection of seeds against wet.

1 Capsules of *Campanula rapunculoides* in dry, 1′ in wet weather. 2 Capsule of *Lychnis diurna* in dry, 2′ in wet weather. 3 Capsules of *Linaria Macedonica* in dry, 3′ in wet weather. 4 Capsules of *Cerastium macrocarpum* in dry, 4′ in wet weather. 5 Capsules of *Silene nutans* in dry, 5′ in wet weather. 6 Capsules of *Pyrola chlorantha* in dry, 6′ in wet weather. 7 Capsules of *Gymnadenia Conopsea* in dry, 7′ in wet weather. 8 Capsule of *Pinguicula vulgaris* in dry, 8′ in wet weather.

of slits arise near the base, while in the Butterwort (*Pinguicula vulgaris*, fig. 340^{8}) the fruit splits into two valves. How all these capsules behave is shown in the portion of the illustration with the shaded background (figs. $340^{1'}$ to $340^{8'}$). Closure is so complete that the entrance of moisture into the capsules is impossible, and the seeds have absolute immunity from premature wetting. Even in the case of capsules with lateral slits, where there is a possibility of moisture entering, the same arrangement prevails, as is well illustrated in the Fragrant Orchis (*Gymnadenia Conopsea*, *cf.* figs. 340^{7} and $340^{7'}$).

Of capsules with openings directed downwards there are but few, and in these the dispersal of the seeds is not accomplished quite in the same manner as in those just described. In the Funkias (*Funkia ovata, Sieboldi, subcordata*, &c.) the pendent capsules open by three valves at their depressed tips, and concurrently some of the seeds are shot out into the air—often to some little distance. Those which remain in the capsule after the sudden opening are not, as one might expect, deposited in a heap on the ground close by, but, being attached to the valves by delicate strings, and having a flattened form, offer considerable surface to the wind, which ultimately loosens them and bears them far away. The fact should be emphasized that in many cases fruits only open under the influence of dry winds, and that the same wind which promotes their dehiscence at the same moment scatters the seeds. This is very well shown by the Scotch Pine (*Pinus sylvestris*). Its cones only separate their scales in the afternoon when the air is driest and a wind is blowing. When the conditions for this are favourable one hears quite a series of noises in the treetop, caused by the separating of the scales, and at the same time the winged seeds go spinning through the air. The scales protect the seeds in this case against wetting, and indeed against other dangers as well. It should be remembered that any protective arrangement is but rarely directed solely against one particular source of danger. An envelope may protect the embryo at one time against the wet, at another against excessive desiccation; sometimes the same envelope may also ward off attacks from undesired guests of the animal world.

Developments on fruits whose chief function is the protection of the seeds against *desiccation* are, on the whole, scarce. In certain portions of Australia the whole vegetation enters upon a sort of summer sleep; during this period no rain falls and the surface of the earth is hardly ever wetted with dew; such a dryness of the air and of the soil prevails that plants are compelled to suspend operations for a while. It has been already explained how the foliage is protected against drying up (*cf.* vol. i. p. 296); but the embryo also, which has arisen within the ovule during the period of vegetative activity, has to be preserved during this period. This is achieved by the massive development of the ovary wall, which in this respect exceeds anything met with in the Floras of other regions of the globe. The seeds of the Wooden Pear (*Xylomelum pyriforme*, see fig. 325^{2} p. 431) are inclosed in a strong pericarp, the wall of which attains a diameter of 2 centimetres, and can resist the greatest dryness for very long periods. So also is it with the seeds of the Australian species of *Banksia* and *Eucalyptus* (see figs. 324 and $325^{13, 14,}$ pp. 429

and 431), the walls of their capsules being exceedingly thick and strong. In not a few Steppe-plants the seeds within are protected by the nature of the inclosing pericarp during the hot, rainless summer season. Remarkable amongst them are the big Umbelliferous genera *Prangos* and *Cachrys*, the schizocarps of which are protected by a thick spongy wall not unlike elder-pith in nature. Preserved within these walls against desiccation, the embryo secures this further advantage, that from the relative largeness and lightness of the fruits they are readily dispersed by the wind over the Steppe.

In dry, dehiscent fruits protection against unfavourable climatic conditions is extended only so long as the seeds remain attached to the parent plant; in achenes, nuts, and schizocarps it lasts longer, however. For in the latter classes of fruit the pericarp accompanies the seed after severance, protecting and aiding it during its passage, and often assisting it at germination. All those developments of the seed-coat, met with in the cases in which the seeds themselves are liberated, are replaced, in these non-dehiscent fruits, by the pericarp or other associated portion—calyx, bracts, and the like. These structures are fashioned so as at once to preserve the seed on its journey, be it by air or water, and to attach it to its germinating-bed by various irregularities of surface—pits, furrows, warts, or even sticky excretions. Further, it is important that arrangements be provided so that the young plant should have access to water at certain spots on the fruit wall, and that on germination it should be able to push out its young rootlet without undue effort, as, for instance, in the Water-chestnut and Bulrush (*cf.* vol. i. p. 607, figs. 144 3, 4, 11, 12, 13).

The stage of development at which the embryo is detached from the parent plant is not the same in all cases. In the Maidenhair Tree (*Gingko biloba*) the embryo is but slightly differentiated at the time when the plum-like seed falls. The egg-cell has been already fertilized, and the enveloping tissues of the seed have matured, but the differentiation of the embryo is postponed till after the seed has fallen. So, too, in Orchids and in many parasitic and saprophytic plants, such as *Cuscuta, Orobanche, Monotropa,* and Balanophoreæ, the embryo, at the moment of severance of the seed, is of the most rudimentary character. But in the majority of Phanerogams the embryo shows a differentiation into plumule, and radicle, and cotyledons. In *Ceratophyllum* the plumule has already slightly elongated and exhibits a number of little leaves, and in *Nelumbium* the leaves show a differentiation into blade and petiole. In the Mangrove Tree (*Rhizophora Mangle,* see fig. 341 1) the embryo attains to a very considerable degree of development whilst still attached to the parent plant. Its root penetrates the wall of the ovary (fig. 341 2) and ultimately attains a length of 30–50 cm. and a thickness of 1–5 cm. and a weight of some 80 grams. Finally, the young plant breaks away from its sucker-like cotyledon and falls into the mud below, where it speedily unfolds a pair of green foliage-leaves (*cf.* vol. i. p. 604). Thus, in the Mangrove Tree, it is not the seed but the embryo which is detached from the parent plant. Comparing the *Gingko* to an oviparous animal, the Mangrove might be regarded as viviparous.

The envelopes which surround the embryo at the moment of detachment vary enormously from plant to plant. The seed of the terrestrial Orchid *Gymnadenia*

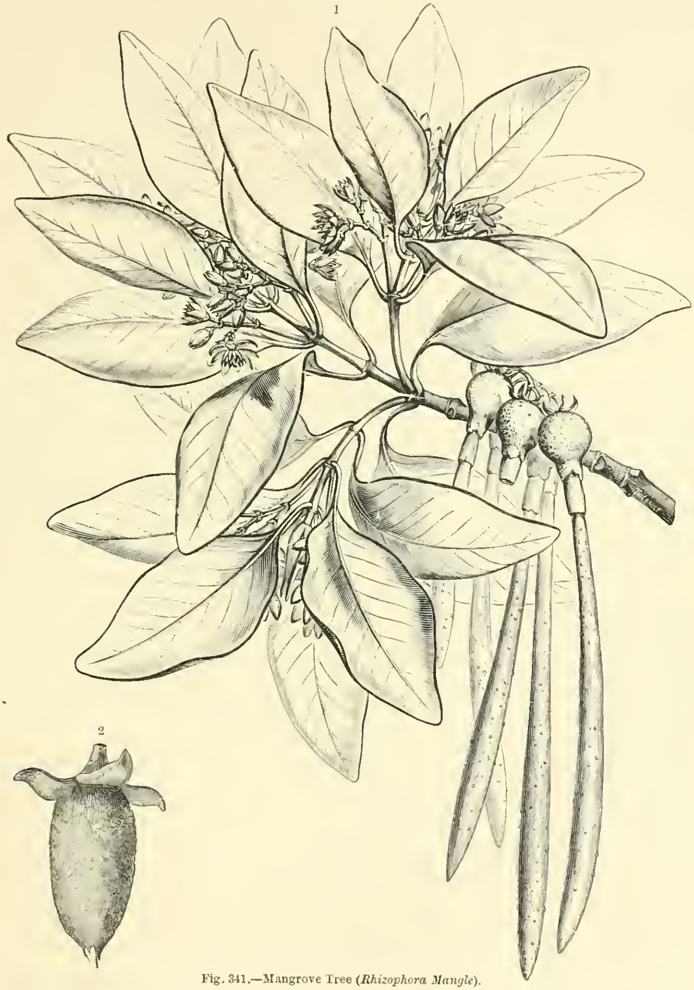

Fig. 341.—Mangrove Tree (*Rhizophora Mangle*).

[1] Branch with flowers and fruits (reduced). [2] Single fruit, the apex of which is being penetrated by the radicle of the embryo. (After Baillon.)

Conopsea measures 1 mm. in length and weighs ·008 gram: that of the Cocoa-nut Palm 11–14 cm. and weighs 800–1100 grams. The Wind Bent-grass (*Apera spica-*

venti) has a grain 1·2 mm. long, ·3 mm. broad, and weighs ·05 grm.; the fruit of the Seychelles Palm (*Lodoicea Sechellarum*) measures 32 cm. by 18–25 cm. by 22 cm., and weighs 4200–4800 grams. The largest fruits are produced by the Cucurbitaceæ; in a suitable soil Gourds attain a diameter of half a metre, whilst fruits of the Melon-pumpkin (*Cucurbita maxima*) have a greatest diameter of over a metre, and a weight of 75 to 100 kilograms. The fruits of the Bottle-gourd (*Lagenaria*) attain under favourable circumstances a diameter of 30 cm. and a length of a metre and a half.

3. CHANGE IN REPRODUCTIVE METHODS.

Fruits replaced by Offshoots.—Parthenogenesis.—Heteromorphism and Alternation of Generations.

FRUITS REPLACED BY OFFSHOOTS.

By *Annual Plants* are understood such as germinate, grow, and conclude their flowering and fruiting within the limits of a single year, and after the ripening of their seeds die away. The activity of these plants is concentrated on the production of a large amount of seed; it is worthy of note that autogamy is frequently met with amongst them, followed by good results. They produce just so many foliage-leaves as are necessary to provide the materials for their flowers and fruits, and reserve-substances for their seeds. With the production of seed, the leaves, stems, and roots perish without forming vegetative buds or offshoots, so that these plants are represented for several months by their seed only. Their rejuvenescence can only occur under favourable climatic conditions where an unimpeded germination is allowed these seeds, and when no interference in the process of development is imposed by men or animals. If the weather be unfavourable in the situations where the plants have established themselves, if the summer be a cold one, so that fruit cannot be ripened, they do not perish at the end of the first year, but prolong their existence till another year by means of offshoots, becoming, for the time being, perennial plants. We may put it, in a manner of speaking, that when the danger of extinction threatens, fruit-production is replaced by offshoots; instead of fruits, tubers, buds, or other shoots are produced, and not infrequently these structures arise in the position usually occupied by fruits. Among the Crassulaceæ there are several annual species (*Sedum annuum, glaucum*, &c.) which normally die away so soon as their seeds have ripened and been dispersed. But when it happens from any cause—as by the premature on-coming of winter—that these processes are interfered with, little rosettes of leaves arise from the base of the stem in close proximity to the root; these are detached, and, as offshoots, continue the life of the plant into another season. Similar phenomena are observed in many other herbs whose flowers or fruit are destroyed by frost. Indeed by experiment these statements can be readily verified. Members of various families (*Poa annua, Senecio nebro-*

densis, S. vulgaris, Ajuga Chamæpitys, Herniaria glabra, Viola tricolor, Cardamine hirsuta, Medicago lupulina), normally annual, are transformed into perennial plants when grown in my alpine experimental garden on the Blaser in Tyrol (Gschnitzthal), at a height of 2200 metres, there being insufficient warmth there for them to produce good seed.

Interference with fruit-production due, in inhospitable situations, to an unfavourable climate, can be artificially brought about by the removal of the flowers from a plant as they appear. Annual plants pruned in this way produce shoots and offshoots which would otherwise have remained undeveloped. These remain living till next year, and if the same treatment be continued indefinitely, a plant, otherwise annual or biennial, becomes perennial. Upon this fact depends the gardening feat of producing little Mignonette trees. Normally the seeds of this plant germinate in a sandy and humous soil, and the plants arising perish in the autumn after flowering and ripening their fruit; but if the inflorescences be carefully pinched off, the stem doesn't die down but produces lateral shoots with the object of developing new flowers. If these flowers be removed year after year, gradually a little tree is formed, with woody stem and branches; and if ultimately it be left alone will cover itself with hundreds of sweet-scented flower-spikes. That a much increased production of leafy shoots and offshoots can be stimulated in perennial plants by this kind of pruning has long been known; by its aid many modes of propagation, as practised in horticulture and agriculture upon cultivated plants, are obtained.

It sometimes happens in nature that a failure of flowers is due to the plants being overshaded. That is to say, many plants growing in shady places either do not produce flowers or their flower-buds do not open and cannot ripen fruit. Such plants produce offshoots from the lower portion of their stem in the form of leafy shoots, runners, &c., if they are able to do so, and this in a very marked degree; in other words, the more flowering and fruit-production is hindered by shading, the more is a development of offshoots promoted. The Willow-herb (*Epilobium angustifolium*) develops its beautiful flowers only in sunny situations, accessible to hive- and humble-bees. The more intense the sunlight, the more vividly are the flowers coloured. Should trees grow up and densely overshadow the Willow-herbs, the flower-buds atrophy before opening and fall away from the axis as small withered structures. Whilst the richly-flowering plants form only short offshoots, these shaded plants produce long, subterranean runners, which seek to penetrate to a distance, out of the circle of shade.

Another remarkable phenomenon in the growth of perennial plants, which flower and fruit copiously under favourable climatic conditions, is that in inhospitable situations, where this is restricted, they propagate themselves very readily by means of offshoots. A Composite, *Nardosmia frigida*, allied to the Butter-bur, is widely distributed over the Arctic regions. Only towards its southern limits does it produce flower and fruit; further north flowers are never met with upon it, but, instead, it propagates itself far and wide by means of offshoots. Similar in its behaviour is another Composite, the alpine *Adenostyles Cacaliæ.* It blossoms and fruits in sub-alpine forests even up to the tree limit, but in high alpine regions, above 2200 metres in altitude, it never flowers, but forms offshoots, and in this way fills little depressions on alpine slopes with its vigorous foliage. The terrestrial form of *Polygonum amphibium* occurs in a little bog close to my country house in the Gschnitzthal in the Tyrol at a height of 1200 metres. For twenty-eight years I have examined this bog every year without ever finding a ripe fruit upon these plants. But it propagates itself with rare luxuriance by means of offshoots and forms a broad girdle around the bog. These plants, *Nardosmia frigida, Adenostyles Cacaliæ,* and *Polygonum amphibium,* grown in a more favourable climate, produce good seed, but their vegetative methods of propagation are so restricted that one might almost suppose them to be different species of plants.

Instances in which flowers are replaced by offshoots or bulbils in the inflorescence may be mentioned in connection with the above. *Polygonum viviparum* and *bulbiferum, Saxifraga cernua, nivalis,* and *stellaris, Juncus alpinus* and *supinus,* and the Grasses *Aira alpina, Festuca alpina* and *rupicaprina, Poa alpina* and *cenisia* occur, it is true, with normally developed flowers and fruits, but in alpine, and especially in arctic regions, where these plants have their head-quarters, one very frequently finds purely vegetative buds or bulbils, which become detached from the parent plant and give rise to new individuals, in place of flowers and fruit. In the Polygonums mentioned little bulbils replace a portion of the flowers. *Saxifraga cernua* usually produces a single terminal flower at the end of its inflorescence, the lateral flowers being replaced by little tufts of bud-like offshoots on short stalks (see fig. 342[3]). These buds, when they fall off, are either still closed (fig. 342[5]), or their thick, fleshy, outer scales are already parted, exposing a little green foliage-leaf. On the ground they soon produce roots and grow into new plants (see figs. 342[6] and 342[7]). In *Saxifraga nivalis* little shoots are formed in place of flowers, each bearing a tuft-like rosette of minute leaves (fig. 342[1]). These rosettes are readily separable, and producing roots from their abbreviated axes, give rise to new plants. So also in the Juncuses and Grasses mentioned, little shoots replace the fruits and come away from the inflorescence. These shoots are produced in *Poa alpina* (see fig. 342[8]) and in most of the other Grasses mentioned, in the following manner. The axis of each spikelet, after producing several glumes at its base, forms green leaves above—as it were a grass-plant in miniature (see figs. 342[9] and 342[10]). Later, these disarticulate, take root, and grow into new plants. More rarely do shoots arise laterally on the axis, in the axils of subtending scales; when this is the case they fall away in the usual manner. The earlier Botanists termed all such Grasses, and indeed all plants which produce bulbils in their inflorescences, *viviparous,* the idea being, that in all of them the seeds germinated precociously whilst still attached to the parent. This view was probably suggested by the common experience of agriculturalists that Rye, Oats, and other cereals sometimes "sprout", *i.e.* that when the spikes are continually wetted by rain about the time of harvest, and the haulm laid flat on the ground, the embryos begin to develop whilst the grain is still in the ear. This premature germination, however, is quite independent of the parent plant, which has given up all its food-materials, and is already dead; the grains, held between the glumes mechanically, are no longer in vital connection with the plant which gave them origin. Their germination between the damp husks is similar to what would occur between pieces of moist blotting-paper. But in these so-called "viviparous plants" the phenomenon is quite different from this "sprouting" of cereals. In them no flowers or seeds are formed, consequently there can be no germination of seeds still united to the parent plant. The detached structures, formerly regarded as germinated seedlings, are in reality little, leafy shoots which have been produced instead of flowers and fruits.

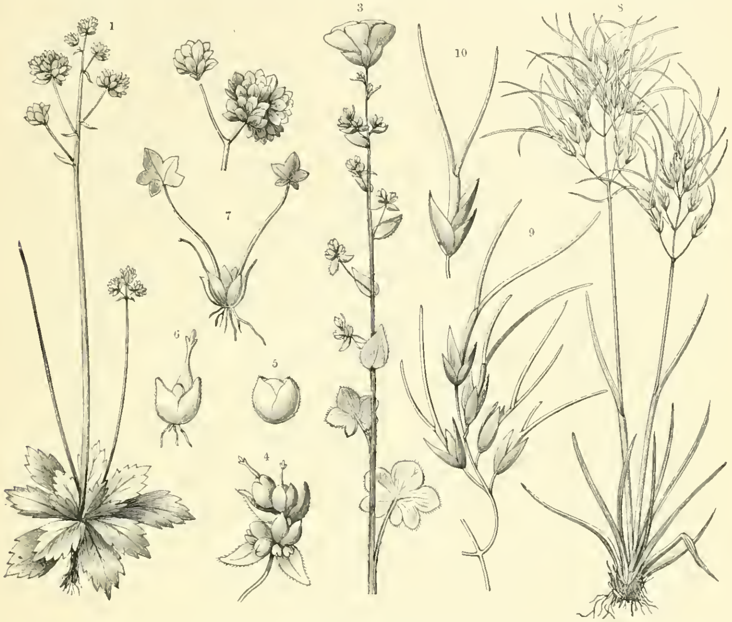

Fig. 342.—Bulbils replacing flowers and fruits.

[1] *Saxifraga nivalis* with rosettes of little green leaves instead of flowers (natural size). [2] Two of these rosettes, enlarged; one of these has become detached from its stalk. [3] *Saxifraga cernua* (natural size). [4] A cluster of bulbils of this plant. [5], [6], [7] Bulbils of same in various stages of development. [8] *Poa alpina* with bulbils replacing its flowers (natural size). [9] A portion of the inflorescence (enlarged). [10] A miniature grass-plant developed between the glumes of a spikelet of *Poa alpina* (enlarged).

The plants which we have just been discussing are essentially forms living in high alpine and arctic regions, that is to say, in regions in which they have but some two to four brief months in the year in which to complete their vital processes. In the majority of plants growing under such inhospitable conditions, the flowers for the following summer are already developed in miniature the preceding autumn, so that on the melting of the snow and the termination of winter the flowers can be at once expanded. When such plants can avail themselves of the warmth of the whole summer they are able to ripen fruit and seed. But it is otherwise with those which produce their flowers on a leafy axis, and which must first form an under-structure on which they can be produced; with these, before flowers can be unfolded, a considerable interval of time must elapse. Their blossoming is delayed, and the ripening of their seed takes place quite at the end of the period of vegetation. There is thus always the danger of early frosts or of the winter-covering of snow intervening before the seeds can be ripened and dispersed. It is in just such plants that preservation and propagation are ensured by a development of bulbils; these structures are more speedily produced than seeds, nor do they require so much warmth; further, they are not so liable to injury from premature advent of winter as are developing fruits. The above-mentioned Polygonums, Saxifrages, Rushes, and Grasses are amongst those which flower relatively late, and are liable, in unfavourable seasons, to a destruction of their seeds. The very frequent substitution in them of vegetative for sexual reproduction would seem to be undoubtedly correlated with this liability of seed to fail. And in not a few steppe-plants the substitution of offshoots for flowers is probably connected with the fact that with them, also, the season is not always long enough for the formation of stem, flowers, and fruit.

It has been previously pointed out that a great many aquatic plants, with roots fixed in the mud and stems and foliage floating in the water, raise their flowers above the surface and avail themselves of the wind and of flying insects for pollination and fertilization. For such plants fluctuations in the level of water must be of considerable moment, and it may well be that if the surface is raised for any length of time, flowering and fruiting are hampered, and, in many cases, rendered impossible. Many marsh and water plants possess, indeed, the capacity of stretching to the surface, the stem continually elongating as the level is raised, until the flowers can be expanded above the surface. But this growth in length has its limits, and it not infrequently happens that, even after an extraordinary elongation of stem and flower-stalk, the surface of the water is not attained. And these flowers in most cases cannot be fertilized under water; if already formed, the flower-buds do not open, but atrophy and fall off without producing fruits. In the little meres of the Black Forest, *Littorella lacustris*, a plant allied to the Plantain, grows; but it only flowers and fruits in very dry years, when the expanse of water is much contracted and the bottom is in large part laid bare. But this is not very often; ten years may pass without the conditions favourable to the flowering and fruiting of *Littorella* obtaining. During the whole of this time the plant must remain barren were it not for the fact that off-shoots, which take root in the mud, are produced instead of fruits. Thus it is able to maintain and propagate itself. Several Pondweeds and Water-crowfoots (*Potamogeton* and *Ranunculus*) behave like *Littorella*, and it would appear that the capacity to propagate by offshoots, so common in aquatic plants, is connected with the impediment to flowering so often presented by a high water-level. *Cymodocca antarctica*, a submerged aquatic plant, which grows in great luxuriance on some parts of the coast of Australia, flowers so rarely that its peculiarly formed bulbils were for a long time regarded as its flowers. Nor has every Botanist seen the flowers and fruits of the Duckweed (*Lemna*); whilst the renowned American Water-weed, *Elodea canadensis*, which has been such an obstacle to navigation in canals, &c., but seldom flowers, and owes its very remarkable propagation and distribution, not to fruits, but to a quick and plentiful production of offshoots.

A dearth of water, also, like a too ample supply, can render fertilization impossible and promote the propagation and distribution of some plants by offshoots to a remarkable degree. In Ferns and Mosses the spermatozoids reach the archegonia, swimming in the water which accumulates on or about the sexual generation of these plants (*cf.* pp. 65 and 68). In the great majority of cases, it is rain and dew which provide the capillary water which invests the plants, and in which the spermatozoids swim. And other conditions in the life of Ferns and Mosses besides fertilization depend on an adequate supply of water; their existence depends on a certain definite amount and on a certain annual duration of atmospheric precipitation. Mosses, and particularly Ferns, have but a restricted distribution in dry localities; or they may be entirely wanting. In humid regions, on the other hand, they attain to a luxuriant growth. The contrast in this respect is striking enough for illustration. Elvend Kuh, a mountain in the interior of Persia, rises to a height of some 3750 metres, and is the culminating point of a considerable plateau. The rainy season is limited to a period of two months, and a rich and well-marked steppe-flora covers the ground. Ferns are absent from an area some 5000 square kilometres in extent, whilst Mosses are only represented by a few species which propagate by means of thallidia, rarely maturing spore-capsules. In the hill country of the West Indies, particularly the Blue Mountains of Jamaica, the vapour condenses every morning, and in the course of the afternoon is precipitated as rain. Here are found some 500 Ferns, and large numbers of Mosses and Liverworts. The level or sloping ground, rocks, the forest floor and decaying tree-trunks, all are covered with Ferns of every shape and size; there are groves of Tree-ferns, the trunks of trees are invested right up to the crown with delicate, green fronds, whilst tiny representatives of the Filmy Ferns (Hymenophyllaceæ) have actually taken up their abode on the foliage-leaves themselves. Within a distance of a hundred paces the plant-collector can find fifty different sorts of Ferns, and as many Mosses.

And between the extremes we have described there are regions with an intermediate climate, of such a character, that although the fertilization of Ferns and Mosses is not perpetually prevented, still wet years are rare, and several years may elapse without the conditions being favourable for it. Such a region is the Hungarian plains, the fields and woods of which produce only two species of Ferns and some dozen Mosses. The latter have almost entirely ceased developing fruits, and propagate themselves for the most part by thallidia, since these can be produced much more simply, and their production is independent of enduring drought.

Certain Ferns must be mentioned in this connection, on the prothallia of which offshoots arise instead of normal, sexually produced embryos. It is true that they form archegonia, but they are abortive, and propagation is asexual. The little Fern-plant arises not from the archegonium but from the tissue in its immediate neighbourhood; the archegonia remain closed, are not fertilized, turn brown, and die. This substitution may be observed in *Aspidium falcatum*, in a crested variety of *Nephrodium Filix-mas*, and in the variegated form of *Pteris Cretica*, frequently cultivated in greenhouses. On the prothallia of normal forms of *Nephrodium Filix-mas*, and on those of wild plants of *Pteris Cretica*, fertilization takes place in the usual way, so that it is possible that the substitution of offshoots for fruits is a result of the conditions of cultivation. To what causes exactly the phenomenon in question may be due, is, however, unknown.

As factors in promoting a substitution of offshoots for fruits amongst the Mosses, other climatic conditions exert considerable influence. But it would lead us too far were we to treat of all these in detail; only a few of the fifty or so examples from the European Moss-flora can be mentioned here. *Leucodon sciuroides*, a Moss which rarely fruits in Northern Europe, produces instead numerous leafy shoots (brood-bodies) which, becoming detached, readily root on a moist substratum (see figs. 196^{9} and 196^{10}, p. 23). *Campylopus fragilis*, again, scarcely ever produces fruits in the Alps; it forms readily separable lateral branches, the leaves of which are carried away by the wind. Any of these leaves falling on a moist spot develops green filaments, upon which little buds arise, originating new leafy Moss-stems (see fig. 196^{11}, p. 23). The case of *Barbula fragilis* and *Timmia Norvegica*, growing in the Alps, is similar to that of *Campylopus*. Of several Mosses the fruits have never been seen; such are *Dicranodontium aristatum*, *Barbula papillosa*, *Grimmia torquata*, *Bryum concinnatum*, and *B. Reyeri*. They are able to maintain themselves in spite of this by vegetative propagation.

In addition to the cases already enumerated, in which climatic conditions, excess or lack of water, &c., promote vegetative as opposed to sexual reproduction, numerous others are known in which peculiarities in the structure of the flowers cause the ovaries to abort, or make it necessary that a formation of offshoots should be initiated if the plants are to be maintained. In this connection certain hybrid Fuller's Thistles and Mulleins (*Cirsium* and *Verbascum*) must be noted. The plants in question are hybrids, that is to say, they are produced by crossing of different species. They flower early in the summer, and have ample time to ripen seed before the on-coming of winter, but in a number of these hybrids, owing to variations in the structure of the flowers and of the pollen, few or no seeds are ripened. On the other hand, just these very plants form aërial buds and subterranean offshoots very freely. *Cirsium purpureum*, a hybrid between

Cirsium heterophyllum and *spinosissimum*, and *Cirsium affine*, a hybrid between *C. heterophyllum* and *C. oleraceum*, are very abundant in many Alpine valleys, and one may find more examples of these hybrids than of their parents in many a meadow. Several of the Fuller's Thistle hybrids, the parents of which are biennial, become perennial by a production of lateral shoots from the leaf-axils at the base of the stem. Here also, as with climatic conditions, we find vegetative propagation replacing fruit-production.

There are also many species, of which it cannot be definitely asserted that they have arisen by hybridization in recent times, which fruit but seldom even when the climatic conditions are in every way favourable for this kind of reproduction. According to agriculturists, there are many kinds of Potato which flower only occasionally but do not ripen fruit, although the flowers and pollen-grains appear quite normal. It is just these Potatoes which are characterized by their rich production of tubers, fruit-formation being in them replaced by vegetative propagation.

That plants, with double flowers, the ovaries of which, under the influence of little insects (*Phytopus*), have undergone a deep-reaching transformation, should ripen no fruits is to be expected and has long been known, as also is the fact that these plants produce buds and offshoots freely. Of special note in this connection is a Bitter-cress (*Cardamine uliginosa*) often met with in damp meadows in the neighbourhood of Vienna, Salzburg, and Ried, growing wild with double flowers. On most of the plants, the fruits of which are abortive, those curious leaf-buds, represented in fig. 200 [4], p. 41, are to be found.

Again, with many species of plants, it may come to pass that the insects which should accomplish their pollination are now no longer prevalent in the region where the plants grow, or indeed have entirely deserted them. This category of plants obviously includes only such forms as are destitute of arrangements for promoting autogamy, in the case of cross-pollination not taking place. In a very considerable number of these plants, flowers and fruits are replaced by offshoots—offshoots of the most varied kinds, including aërial and subterranean tubers, bulbils, green leafy shoots, and, in rare cases, little bud-like structures, from each of which a thick, fleshy root arises in such a manner that the greater part of the offshoot consists of a root.

As all these varieties of offshoots will be dealt with in a later chapter devoted to the distribution of such structures by wind, animals, and special mechanisms, it must suffice to speak here of a very few cases. Growing in sunny spots, the yellow flowers of the Lesser Celandine (*Ranunculus Ficaria*) are occasionally visited by little pollen-eating beetles, by flies and bees; under these circumstances heads of fruit are ripened here and there from the flowers. But in shady places, beneath bushes, and on the dark forest floor, these insect-visits are much rarer, and almost all the flowers fail to ripen fruit. These shaded plants, however, develop little bulbous bodies in the axils of their upper foliage-leaves, which become detached on the withering of the shoot and give rise to new plants (see fig. 343^{3}). Those which ripen fruit, on the other hand, form no offshoots, or only very few. In the Coral-root (*Dentaria bulbifera*, see figs. 344$^{1, 2, 3, 4, 5,}$) a similar state of affairs prevails. Pollination is accomplished only by insect-agency, and where insects fail no fruits are ripened. The plant grows sometimes near the sunny border of young Beech-plantations where insects are plentiful, and also in the forest of older growth in whose dusky glades bees and flies, humble-bees and butterflies are rarely met with. Those which grow in the better lighted, younger portion of the wood ripen their cruciferous capsules, but the others, in the deep gloom, are free of insects and blossom in vain. Their ovaries for the most part abort and fall away, and only occasionally do their fruits come to maturity (*cf.* fig. 344^{2}). But in proportion as fruit-production is arrested, vegetative propagation by bulbils is promoted; large bulb-like buds are formed in the leaf-axils, which disarticulate as summer advances and the shoot begins to fade; they are detached by the wind as it sways the stems, and falling on the moist floor of the forest take root (fig 344^{4}) and give rise to subterranean rhizomes (fig. 344^{5}). Some plants

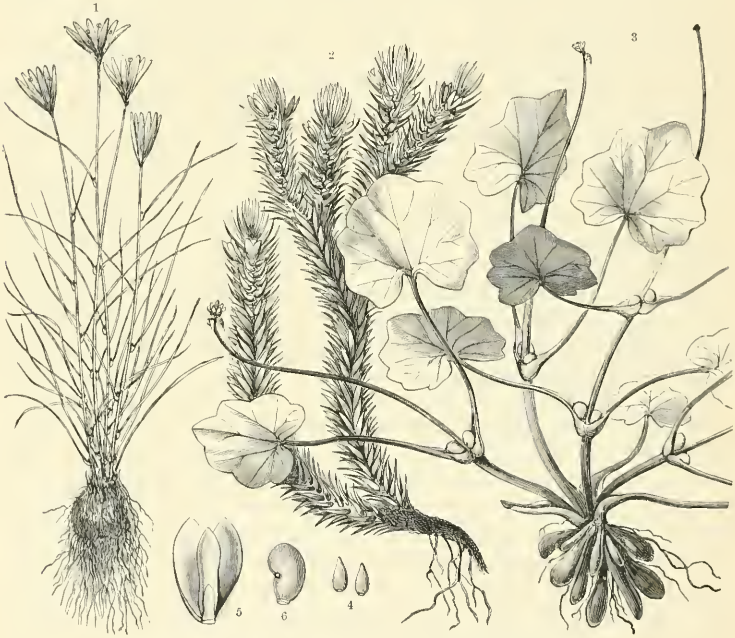

Fig. 343.—Flowers and fruits replaced by tubers and bud-like offshoots.

^{1} *Gagea Persica.* ^{2} *Lycopodium Selago.* ^{3} *Ranunculus Ficaria.* ^{4} Bud-like offshoot from the leaf-axil of *Gagea Persica.* ^{5} Bud-like offshoot of *Lycopodium Selago.* ^{6} Tuber-like offshoot of *Ranunculus Ficaria.* $^{1, 2, 3}$ nat. size; $^{4, 5, 6}$ enlarged.

occur in these shady spots which bear no flowers at all, and depend entirely on a production of these offshoots (*cf.* fig 344 [3]).

There are two forms of Orange Lily indigenous to Europe. One (*Lilium croceum*), occurring especially in the Pyrenees and South of France, almost always ripens fruits and forms no bulbils in its leaf-axils. The other (*Lilium bulbiferum*), found in the valleys of the Central and Northern Alps, hardly ever fruits, but is characterized by the bulbils it produces in the axils of its leaves; bulbils which disarticulate in autumn and are scattered by the wind. But there is no difference noticeable in the structure of the flowers in these two Orange Lilies, and it is difficult to explain their difference in mode of propagation, save on the assumption

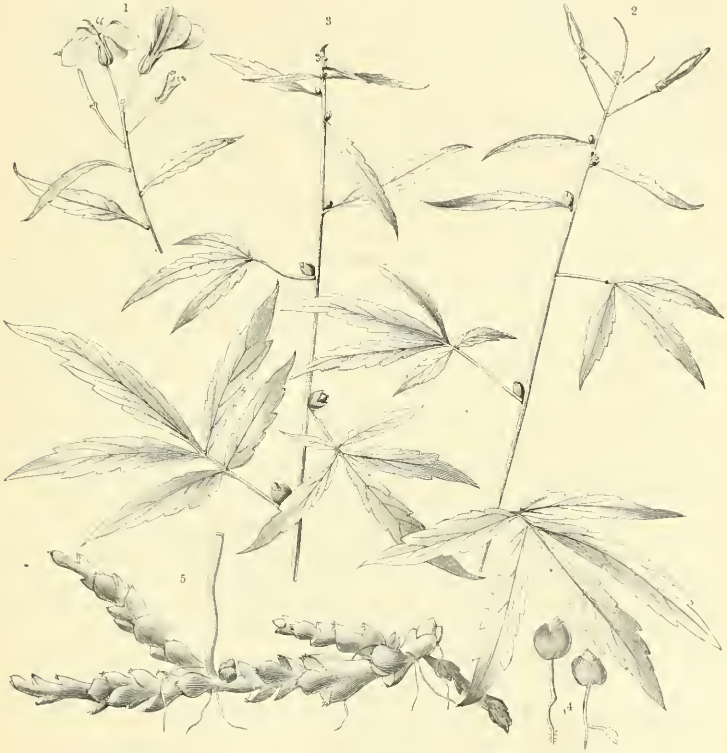

Fig. 344.—Flowers and fruits replaced by bulbils. The Coral-root (*Dentaria bulbifera*).

[1] Inflorescence. [2] Leafy shoot on which two fruits have ripened; bulbils in the axils of some of the leaves. [3] Leafy shoot whose inflorescence has atrophied; bulbils in the axils of all the leaves. [4] Detached bulbils forming roots. [5] Rhizome of *Dentaria bulbifera*.

that in the regions where *Lilium bulbiferum* grows those insects are wanting which should convey its pollen from flower to flower. As the Orange Lily possesses no arrangements for autogamy, no fruits are formed in the absence of insect-visits. It appears that this plant has lost the capacity for autogamy; at any rate if a stigma be pollinated with pollen from the same flower, on plants in a garden, no result follows. On the other hand, offshoots in the form of numerous bulbils are produced by *Lilium bulbiferum*, by means of which it is propagated and dispersed. In several valleys of the Central Alps it does not flower at all, and thus obviously depends entirely upon its bulbils for propagation.

Gagca Persica (fig. 343[1]) a member of the Liliaceæ, repeats several of the peculiarities met with in the Orange Lilies. The stem of this little bulbous plant terminates in a flower which, in the absence of insect-visits, withers without setting fruit. Little buds arise in the axils of its filamentous foliage-leaves. With the atrophy of its fruits these grow into little bulbils (fig. 343[4]); but if fruit be formed these buds for the most part atrophy. Nor must we omit to mention the ally of this plant, *Gagea Bohemica*, belonging to the flora of Central Europe. From its specific name, *Bohemica*, it might be supposed that it is solely met with in Bohemia; this is not so, it was first discovered there, but is distributed widely over Persia, Asia Minor, Southern Russia, and the Balkan Peninsula. Further west *Gagea Bohemica* occurs rather sparingly, in Bohemia and in the neighbourhood of Magdeburg—these occasional occurrences being no doubt a last lingering remnant of a Steppe-flora which at some former period extended to the Harz Mountains. We shall later have opportunity of explaining how this Steppe-flora has retreated eastwards and been replaced by other communities of plants; here we may mention that this retreat of the Steppe-flora was accompanied by a retreat of the Steppe-fauna. The Steppe-antelope, Steppe-marmot, Steppe-porcupine, rat-hare, &c., which existed in those times in Central Germany, have long forsaken this region, and we have good grounds for assuming that the insects of that period have also migrated. It is certainly remarkable that this Steppe-plant, *Gagea Bohemica*, the flowers of which are adapted to insect-pollination, and in which autogamy does not occur, should never ripen its fruit and seeds in these scattered localities of Bohemia and Germany. One can hardly help supposing that this abortion of fruits is due to the absence of those Steppe-insects which were formerly, in all probability, distributed also over Bohemia and Germany. Whatever be the explanation, it is a fact that these isolated western representatives have never been known to ripen fruit and seed. But instead, at the bases of the leaves, bulbils are formed which fall away and root, maintaining and propagating the species.

Equally instructive is the case of one of the Chickweeds, *Stellaria bulbosa*, now confined to a restricted area in Carniola and Croatia. It flourishes there in the deep, black humus of the forest floor, preferably on the banks of little water-courses, forming here and there dense, luxuriant masses. Its flowers unfold quite early in the spring; and although they are fairly conspicuous, standing up white from the green background, they are rarely visited by insects. The few flies which come to them seem to be undesired guests; they promote no pollination, and fruits are not ripened. I have sought vainly for fruits in the neighbourhood of Laibach in Carniola where *Stellaria bulbosa* is very abundant; there were thousands of faded flowers, but never a fruit with ripened seeds. Its filamentous subterranean stems, on the other hand, bear innumerable white buds; and if one digs up a handful of the black woodland mould, it simply teems with these offshoots. The little streams in spate after a thunderstorm often wash away some of the humus from their banks, exposing and carrying away these little buds in the whirl of waters. Ultimately they are left somewhere, high and dry; and if the conditions are favourable, take root and establish themselves in these new localities. In this manner, at the present time, is *Stellaria bulbosa* propagated and distributed. We cannot suppose things have always been thus; we are driven to the conclusion that in this case, also, the plant, much restricted as to its distribution, is a fragment of a vanished flora. In the Karst district of Carniola and Croatia such fragments are not infrequent, and when one puts all the facts together one may well conclude that this flora has retreated or been driven back in a south-easterly direction at a period not very remote from our own. Accompanying these changes there may well have been changes in the distribution of the insect-fauna, and those insects which formerly visited the now rare *Stellaria bulbosa* of the Karst, and were of great importance to it, may have migrated eastwards or indeed have become extinct.

PARTHENOGENESIS.

At the commencement of the Nineteenth Century the attention of Botanists was directed to a certain aquatic plant, widely distributed in the Old World from Ireland to China, and from Finland to Northern Africa, and occurring very commonly on the Baltic littoral and its islands. This plant was *Chara crinita*, one of the Characeæ, which flourishes in brackish water near the sea, and here and there in salty, stagnant inland lakes. In whatever ditch or pool it takes up its abode it occurs in large quantities, and forms, like many of its allies, extensive and luxuriant masses. It is an annual plant, dying off in the autumn. Next spring young plants arise from the oogonia which have passed the winter on the muddy bottom—and so from year to year. *Chara crinita* is diœcious, that is to say, some plants bear oogonia only, others antheridia (*cf.* p. 62). Whilst in the generality of diœcious Characeæ the male and female plants grow in one another's immediate vicinity, in *Chara crinita* such a distribution is extremely rare. Hitherto, male plants have only been found at Courthezon, near Avignon, in the South of France; near Gurjew on the Caspian Sea; and at Salzburg, near Hermannstadt, in Siebenbürgen (Hungary). I have myself found plants bearing antheridia in some little salty pools near Soroksar, south of Buda-Pesth in Hungary. In the North of Germany on the shores of the Baltic, where *Chara crinita* is very abundant, a male plant has never been found. Nor have Botanists been wanting in their endeavours to find such, should any occur in this region. The Dassower See near

Lübeck, the neighbourhood of Warnemünde near Rostock, the two Jasmunder Boddens (inland branches of the sea), on the island of Rügen, and the Wanger Wieck near Stralsund, where *Chara crinita* is exceedingly plentiful, have been repeatedly searched for male plants but in vain. And the female plants also have been examined in case, perchance, an occasional antheridium might occur upon them, as in the monœcious species of *Chara*. Thus we may take it as established that in the Baltic region no antheridia and consequently no spermatozoids are developed. Nor was the attempt successful to explain the matter on the supposition that at the time of fruiting spermatozoids were brought by water-birds from Hungary, the Caspian, or the South of France. In the Baltic the egg-cells of *Chara crinita* remain unfertilized in their oogonia; the latter fall off in autumn and, without stimulus from any spermatozoid, germinate in the spring. We have here an instance of what Zoologists have termed *Parthenogenesis*. It has been demonstrated with certainty that new individuals arise from unfertilized eggs in the Spruce-gall Aphis (*Chermes*), in plant-lice (*Aphis*), and in many bees, wasps, &c. Also, in the Silk-worm Moth and in *Solenobia*, larvæ arise from unfertilized eggs and these pupæ give rise only to females. This is of interest in that from the unfertilized oogonia of *Chara crinita* only individuals with oogonia arise.

Cases similar to *Chara crinita* are thought to exist in several plants found in water or on moist substratums. In the genus *Syzygites* (now included in *Sporodinia*), a mould-like Fungus belonging to the Mucorini (*cf.* p. 54), the protoplasm in the conjugating branches forms the starting-point of new individuals without any actual fusion or conjugation taking place. So also in the Saprolegniaceæ it often happens that the egg-cells in the oogonia form new plants without being fertilized; probably renewed investigations will bring to light similar relations in many Peronosporeæ, Siphonaceæ, &c.

Amongst the Mosses parthenogenesis does not seem to be so very rare. In them, as in Characeæ, fertilization is accomplished by means of water; the plants are wetted by rain and dew, and this moisture is held by capillarity in the chinks, &c., between the leaves. The fertilizing spermatozoids travel some distance, swimming through the water to reach the archegonia. This distance is not very great in many forms, and these ripen their fruits freely. But there are several species in which only male plants occur in one locality and female plants in another—it may be hundreds of miles away. Such species are *Paludella squarrosa*, which occurs in North Tyrol with antheridia, and in Bohemia with archegonia only; *Grimmia Hartmanni*, found in the Alps with antheridia, and in the Carpathians with archegonia. *Neckera Besseri*, *Aulacomnion turgidum*, *Bryum alpinum* and *B. Duvalii*, *Didymodon ruber*, *Barbula recurvifolia*, *Amphoridium Mougeotii*, *Mnium insigne*, *Pterogonium gracile*, *Hypnum rugosum*, and *Thuidium abietinum* are further examples of which we cannot treat here in detail. As it is impossible for the archegonium of a Moss in the Carpathians to be fertilized by a spermatozoid from an antheridial plant in the Alps, and as fruits are ripened nevertheless, though not very abundantly in truth, it may well be that these are cases of parthenogenesis, cases, that is, of egg-cells which continue their development unfertilized.

Amongst Flowering Plants, also, cases are known in which ovules sometimes, without ever being fertilized, form embryos which grow up into healthy plants. An instructive example is the case of *Gnaphalium alpinum* (=*Antennaria alpina*), a perennial Composite nearly allied to both the common Cat's-foot (*Gnaphalium dioicum*) and *Gnaphalium carpaticum* of the Alps and Carpathians. This plant occurs in Scandinavia from Telemarken to Havosund (59° 52′ to 71° north. lat.), and in Russia from Finland to the Kola Peninsula, also in Arctic Siberia, in Arctic America, in Labrador, Melville Peninsula and the whole Arctic Archipelago, in Greenland between the parallels 60° and 72° north lat., finally in Iceland. Thus it is distributed in a zone surrounding the North Pole, some 12° in breadth. It is absent from the mountains of Central and Southern Europe, and is not known to exist, for certain, on the mountains of Central Asia. In these northern latitudes *Gnaphalium alpinum* is exceedingly common, occurring abundantly in innumerable localities. But it is a remarkable fact that neither in Arctic America nor in Arctic Asia has a plant producing pollen ever been found. In the Scandinavian Flora once, in the year 1842, a pollen-bearing plant was alleged to have been discovered; but this has been discredited. A large number of Botanists, thoroughly familiar with the Scandinavian Flora, are unanimous in saying that they have never seen stamen-bearing flowers, and that ovaries only occur. I have myself obtained plants of *Gnaphalium alpinum* from the Dovrefjeld in Norway, and have flowered them in my garden. Every flower produced an ovary but no pollen, so that the possibility of pollination was excluded. A number of achenes ripened containing good seeds, and these, carefully cultivated, produced plants, in all respects similar to the parent form. When these young plants flowered the same phenomena occurred. Thus, one has good grounds for asserting that *Gnaphalium alpinum*, throughout the wide area of its distribution, is propagated parthenogenetically, and that its reproduction is not hindered by the absence of pollen-bearing plants.

Another plant, of which it has been long known that embryos arise in its unfertilized ovules, is a species of Dog's Mercury (*Mercurialis annua*, see fig. 345), one of the Euphorbiaceæ, widely distributed in fields and gardens, in hedge-backs and waste places, throughout Central Europe. Some individuals of this species produce staminal flowers only (fig. 345 [1]), others, female flowers only (fig. 345 [2]). Its dust-like pollen is conveyed to the stigmas by currents of air, and the ovaries of the female flowers ripen seeds freely as the outcome of fertilization. But female plants have often been cultivated in pots by themselves, with the result that they also ripened seed, though smaller in amount than when there is access to pollen, as is the case with plants growing freely in the open. These results were much canvassed, and discredit thrown upon them by many. It was urged that the dust-like pollen might have come from afar, in the air, and have entered the conservatory in which the experiments were conducted; and again it was pointed out that many female plants of *Mercurialis annua* bear here and there a male flower alongside the female ones. For the refutation of these objections fresh experiments were necessary in which every precaution should be exercised to eliminate sources of error. Such experiments should be conducted in some district in which for miles around the plant did not grow wild, so that the possibility of casual introduction of pollen might be excluded. Fulfilling this requirement is the Central Tyrol, from which both the annual and perennial species of Dog's Mercury are absent. Accordingly I repeated in my upland garden in the Tyrolese Gschnitzthal the cultural experiments originally carried out in 1833 by Ramisch at Prague. Every precaution was taken to avoid sources of error; and in particular were all plants destroyed which showed a tendency to produce male flowers, and the utmost vigilance kept lest an isolated male or hermaphrodite flower should make its appearance anywhere. At the time when the stigmas were ready to be pollinated there were no pollen-grains of this plant anywhere in the neighbourhood for miles around, so that the possibility of such a pollination was excluded. Nevertheless the ovaries set and fruit was ripened, and from the seeds young plants arose.

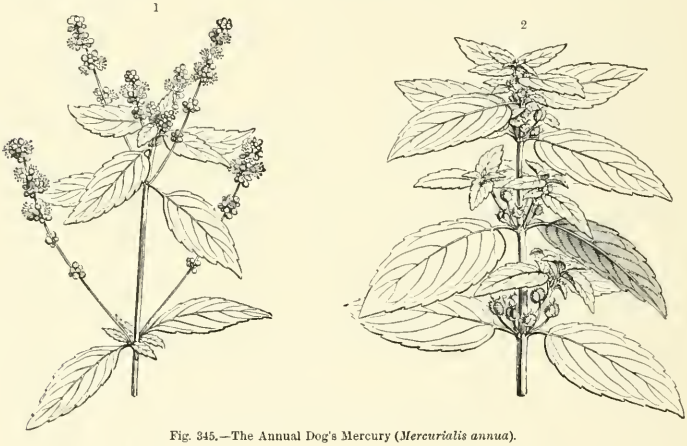

Fig. 345.—The Annual Dog's Mercury (*Mercurialis annua*).

[1] With male flowers [2] With female flowers.

Another plant, also belonging to the Euphorbiaceæ, in which embryos arise in unfertilized ovules, is *Cœlebogyne ilicifolia.* It was introduced into Europe from the bush of Eastern Australia in 1829, and is now in general cultivation as a hot-house plant in Botanic Gardens. The first specimen introduced bore only female flowers, and all the plants which have been raised from this specimen, and distributed over Europe, resemble it in this respect. Plants of *Cœlebogyne* with male flowers are unknown in European conservatories. The possibility of such occurring on the female plants (*cf.* p. 300) has not been ignored, but they have never been detected on the plants used for observations; consequently its own pollen has never had access to the stigmas of the plants in question. In spite of this, ripe seed has been obtained and new plants raised from it, which, in their turn, bore only female flowers. Nor do these new plants differ in any way from the plant originally introduced; this observation is of importance, as it might be suggested that they were hybrids, that the pollen of some other euphorbiaceous plant had reached the stigma, there produced pollen-tubes and fertilized the ovules of *Cœlebogyne*. But this is not so, otherwise the offspring would give some indication of such origin. And the plant itself gives indication that it is not fertilized by any pollen. If a plant of *Cœlebogyne* be kept apart where no pollen has access to it, it can be noticed that its stigmatic lobes remain quite fresh for a long time, even till the ovary begins to swell. Only later do they fade, when the seeds are well advanced. This observation is of value since in ordinary cases the stigmas fade very soon after pollination, and it is only unpollinated stigmas which retain their freshness (*cf.* p. 285). In view of these oft-confirmed results, from which all possible source of error has been eliminated, we may conclude that the ovules of *Cœlebogyne ilicifolia* are able to produce embryos without the co-operation of the male protoplasm.

We may now consider whether the instances just described can be regarded as cases of true fruit-formation. As the essence of fruit-formation is a union of ooplasm and spermatoplasm, or in other words, fruit-production must be preceded by fertilization, and as this condition is not fulfilled, these structures are not true fruits. In the absence of fertilization, we must regard these reproductive bodies as brood-bodies, or a special form of offshoot. As has been previously mentioned (p. 44), brood-bodies can arise from any portion of a thallus, from any portion of the stem, and from leaves of the most various kind. A brood-body can originate from the protoplast of a cell of a Lichen-thallus or of a Moss-leaf, from one in the root of an Ash-tree or in the stem of an Orange Lily, on the margin of an Orchid-leaf, or over the midrib of a Begonia-leaf; why not also from the protoplast in the oogonium of *Chara crinita*, or in the archegonium of a Moss, and in the ovules of *Gnaphalium alpinum*, *Mercurialis annua*, and *Cœlebogyne ilicifolia*? Experience shows that in the great majority of cases, both in the Cryptogams and in the Phanerogams, the young commencements of the fruits abort if the ooplasm be denied the spermatoplasm which should fertilize it; but it also shows in unmistakable manner that in a few plants the ooplasm does not die even in the absence of fertilization.

Without entering upon profitless speculations belonging to the domain of Nature-philosophy, we may discuss the question of the possible reasons for the curious behaviour of the "fruits" in these cases. And first of all it may be observed that all the plants exhibiting the phenomenon of parthenogenesis are diœcious. For such plants a crossing with other individuals is alone possible. But what occurs should a crossing in such plants be impeded from any cause? It seems contrary to the economy of plants that the egg-cell, produced at great expense of energy, and in a sense the culmination of a plant's activity, should wither away unproductive. Plants with hermaphrodite flowers can, if denied crossing, resort to autogamy. But this is of course impossible with diœcious plants; instead of autogamy the formation of embryos in unfertilized oogonia and ovules is a possibility open to them, whereby their outlay of material and energy shall not be wasted. Diœcious plants, which are likewise annuals, are especially liable to the danger of extinction in the absence of pollen and consequent fruit-production; for them the death of the individual may connote the disappearance of the species. Against such possibilities many precautions exist amongst plants, notably the formation of offshoots or brood-bodies; the leafy shoots arising from these structures preserve the plant from such a contingency. In the same way we may regard the formation of brood-bodies in the ovules of diœcious plants as a means contrived to prevent the extinction of the species. The fact that brood-bodies are formed in the ovules of not a few diœcious plants to which pollen has not ready access, supports this view. There has been a specimen of the Californian bush, *Obione halimifolia* (an *Atriplex*, Chenopodiaceæ), for many years in the Vienna Botanic Garden. This plant is diœcious; the Vienna plant bears only female flowers, and pollen is not accessible within hundreds of miles. Its stigmas remain unpollinated, and its ovules unfertilized. But as the autumn draws in, the ovaries of this plant begin to swell, and the perianth which ensheaths the ovary expands, and what appear to be fruits are formed. But these fruits are what we call "deaf"; no signs of an embryo are to be found within. Thus, in this plant, no brood-body has been produced; it is impossible to say whether or no, at some former period, this plant ripened brood-bodies in its unfertilized ovules. Why the male plants of *Chara crinita* are absent from the Baltic, and those of *Gnaphalium alpinum* from the Arctic regions, are puzzles as yet unanswered. In *Chara crinita* it is only on the coast-regions that male plants are wanting; inland, male and female plants grow side by side. Possibly, climatic conditions and the vicissitudes to which our existing Flora has formerly been subject have brought this about, but we lack the data for continuing the discussion further.

If, in the plants enumerated, parthenogenesis be but a special case of offshoot formation, it is a matter of indifference which cells within the ovule are the starting-points for the brood-bodies. In *Cœlebogyne,* in addition to the egg-cell, other cells belonging to the wall of the embryo-sac are concerned in the production of brood-bodies. Cells quite outside the embryo-sac can also initiate these offshoots; in which case they project as little papillæ into the cavity of the embryo-sac, where they continue their development. In this way several embryos may arise side by side, a condition which has been termed *Polyembryony.* This phenomenon occasionally takes place in the ovules of hermaphrodite flowers, in which a normal pollination and passage of pollen-tubes to the micropyle occur. This is the case in certain Liliaceæ, polyembryony having been observed in species of

Funkia and *Allium*, in both of which normal fertilization takes place. It is interesting to note that in the case of *Allium odorum* recent investigations show that the accessory embryos arise actually from the *antipodal cells* (*cf.* pp. 416, 417), *i.e.* from cells at the base of the embryo-sac which, in ordinary cases, simply atrophy. Usually one embryo only arises from this source, but occasionally all three antipodal cells develop into embryos. The ultimate fate of the embryo arising (by fertilization) from the egg-cell and of those arising from the antipodal cells has not been ascertained.

A peculiarity of parthenogenesis consists in the fact that the brood-bodies arising in the ovules assume the form of embryos, not distinguishable from embryos resulting from fertilization of an egg-cell. Little tubers or buds produced in the ovary in places of ovules, as in *Amaryllis* and *Crinum* (*cf.* p. 44), partake of the nature of branches of the plant producing them; but the offshoots which arise within ovules are not branches but young plants, provided with root, stem, and leaves, and they are nourished by a special tissue which cannot be interpreted as a portion of the axis of the young plant. These offshoots arising within the ovule possess a new and independent axis, and herein exhibit an essential difference from the offshoots described in the last chapter. Why these offshoots in the ovules always assume the guise of embryos is a problem which we shall not solve, perhaps, until we have more knowledge as to the essential differences in property between the protoplasm of the ovule and that of other plant-organs.

HETEROMORPHISM AND ALTERNATION OF GENERATIONS.

A sight of the sea-anemones and ever-varying polyps and corals, viewed through the blue-green waters of a shallow bay, at first suggests a kaleidoscopic assemblage of blossoming plants. At a distance the crowns of expanded tentacles resemble red and purple Asters or the flowers of Mesembryanthemums; the skeletons of these organisms are not unlike, in their ramification, the branching of some tufted plant. The corals and polyps, like plants, are denied free movement, and like red and other seaweeds, are attached to their stony substratum. Very appropriate then, in view of their characteristic appearance, is the name of Zoophytes which Zoologists gave to these animals.

And in their internal structure and mode of life they present certain remarkable points of resemblance to plants. In many species the single individuals which are joined together into a colony behave quite like the organs of a body, or the members of a single organism which discharge different functions. There is a division of labour amongst the individuals or polyps of the colony. One branch of the colony is concerned in the acquiring of nutrition, another in reproduction, yet they have a common digestive cavity, so that the juices obtained by one portion may be shared by others which cannot take them up from the environment for themselves. To this differentiation amongst equivalent members we may apply the term *Hetero-*

morphism; it will be seen in the sequel that Heteromorphism is a condition of wide occurrence amongst plants.

Zoophytes propagate themselves in two ways. They may produce buds which grow into new individuals, just as buds arise on the branches of a tree and grow into new branches; and, like the latter, the products of these buds remain attached to the part of the colony producing them, so that ultimately the extent of the colony is considerably augmented. In many Zoophytes, especially in the Polypomedusæ, certain branches of the non-sexual polyp-form assume the form of cups or capsule-like structures in which buds arise which grow into disc-like, free-swimming medusæ, with a crown of tentacles. These medusæ contain sexual organs, and from each of their fertilized eggs an embryo arises which becomes attached to the sea-bottom, and grows either into a non-sexual polyp or into a group of sexual medusæ. In the last-named event the pear-shaped embryo, after swimming about for a while, becomes attached by its pointed end. On its body arise a number of ring-like furrows, which gradually deepen until the cone-shaped embryo is segmented into a number of transverse discs. Ultimately the cone disarticulates and the discs swim away as medusæ. These medusæ are sexual persons, and from the fertilized egg-cells, either sexual or non-sexual generations may arise. This alternation of sexual and non-sexual persons is known as *Alternation of Generations.*

Thus within the limits of the Zoophytes we see displayed two entirely distinct things. First, heteromorphism, which gives us equivalent polyps on the same colony, variously modified for the discharge of different functions; secondly, alternation of generations, in which medusa-forms (sexual persons) arise by a process of budding from polyp-forms (asexual persons), and give rise, by a sexual process, to fresh polyps. Alternation of generations is an alternation of sexual and asexual individuals, the one giving rise to the other.

Both these phenomena are widely manifested amongst plants. The plant-body amongst the Flowering Plants may be regarded as an assemblage of shoots. Each shoot or branch-system consists of a series of members, of which the upper and younger ones are developed with the assistance and co-operation of the lower and older. These shoots are all united together, and the tissue which unites them, with its conducting-tubes and air-lacunæ, may be regarded as an organ common to them all. From the fact that the several shoot-members have the capacity of independent existence, when separated from one another, they have been regarded as individuals and termed "Anaphytes" (*cf.* p. 6). Shoots, united together into a plant-body, possess a common household, and division of labour is manifest amongst them. The Anaphytes of the foliage region serve especially for the preparation of food-stuffs, those of the flowering region for the production of sexual cells and fruits. Shoots of the latter kind are termed flowers, of the former foliage-shoots. Shoots arise from buds, and these may be similarly distinguished into flower-buds and foliage-buds. Those which arise from foliage-buds remain, for the most part, attached to the plant-body, appearing as branches of the same; those, on the other hand, which arise from flower-buds ultimately disarticulate, leaving a scar. Thus we see the shoots of a plant-body are variously modified, and we may speak of a *heteromorphism* in this connection analogous to that existing amongst the polyps of a coral.

It not infrequently happens, amongst purely foliage-shoots, that the lateral shoots (or anaphytes) bear foliage quite unlike that borne by the shoot that gives them origin. In many perennial shrubs and trees a long series of asexual shoots arises, of which the lowest and highest are so different, that one might easily suppose them to belong to different species of plants; or that a gardener had grafted a bud of another species upon the plant. The shoots of young Ivy plants (*Hedera Helix*), whether creeping on the soil of the forest-floor, or climbing up the trunks of trees or steep rock-faces, bear shortly-lobed, white-veined, dull-looking leaves, and produce a large number of attachment-roots which hold the shoot to the substratum. The shoots of an old plant, however, developed high up on the tree crown, or over the top of the wall, bear bright shining, heart-shaped leaves without conspicuous veins, nor do they produce roots at all. It is this latter class of shoots alone which bring forth flowers; the creeping shoots never do so (*cf.* vol. i. p. 709).

This contrast between the appearance of the shoots of a young plant and those produced in later years is much more marked in the Aspen (*Populus tremula*). The foliage-leaves of the first year's shoots are triangular, cordate at the base, and only shortly stalked, they are also hairy on the under surface; those arising on the shoots of a thirty-year-old Aspen are circular in outline, smooth on both sides, and provided with long petioles. Similar is the case of many Willows, Oaks, and Myrtaceæ; in the last-named family the Australian *Eucalyptus globulus* is worthy of mention. The leaves on its first year's shoot are sessile and cordate at the base, whilst on the grown tree they are stalked and curved like a boomerang. Very marked, again, are the differences in the character of the foliage-leaves on the successive shoots of the Junipers (e.g. *Juniperus excelsa, japonica, phœnicea, chinensis*, and *Sabina*). The leaves on the younger branches (for the first ten years about) are acicular, stiff and spreading; those on the shoots of later years are short, scale-like, and closely imbricating. Worthy of note in this connection is the contrast of long and short branches seen in many Conifers, *e.g.* the Larch (*Larix*). Though the actual leaves are not dissimilar, their insertion is, and the length of the shoots producing them. Whilst the short branches do not attain a greater length than 1 centimetre, the long branches reach to 15 or 25 cm.; to this contrast is due in large degree the altogether peculiar physiognomy of the Larch-tree, as shown in fig. 354 (*cf.* also, fig. 337 [1], p. 443).

The fruit-trees in our orchards are some years covered with blossom, and, with a propitious summer, they are weighed down with fruit in the autumn. Such "bumper" years are generally followed by a series of lean years, in which little fruit is ripened, or flowers are hardly produced at all. The same thing is observed in forest trees. There is a saying that Firs and Larches only form their cones in plenty once in seven years. This is so far right in that a good fruiting year is followed, in these trees, by several sparing ones; so much so that it suggests that the trees are exhausted by the heavy production and require time in which to recover, and, by the formation of non-flowering shoots with green foliage, to manufacture and lay by stores of food-material. So also in many low herbs. Now and then the Orchids in the meadows flower in immense profusion, and we say it is a good "Orchid year"; then follow years in which, in the same localities, hardly an orchid-flower is to be found.

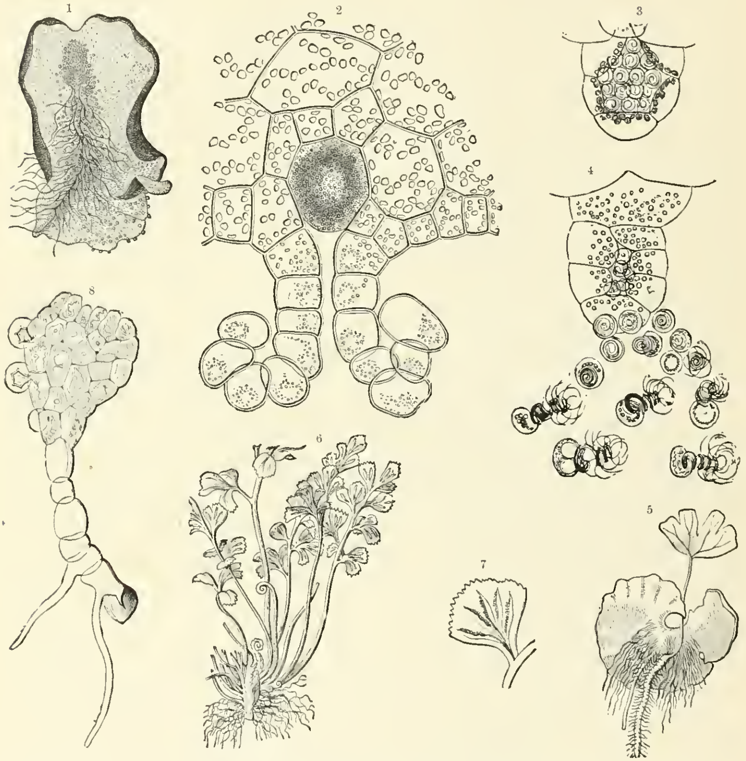

Fig. 346.—Alternation of Generations in Ferns.

[1] A Fern-prothallium seen from the under side; archegonia are present amongst the rhizoids and towards the sinus at the top, antheridia on the margin below. [2] Longitudinal section of an archegonium showing the egg-cell (shaded) in its ventral portion. The canal leading to the egg occupies the neck-portion. [3] Longitudinal section of an antheridium showing the spermatozoids coiled up within. [4] Antheridium discharging its spermatozoids. [5] Commencement of the asexual generation. The first simple frond of the young fern-plant (sporophyte) is held aloft, whilst a root descends into the ground. The young fern-plant is still attached to the prothallium. [6] Complete sporophyte of the Wall-rue Spleenwort (*Asplenium Ruta-muraria*) with its fronds showing sori. [7] Under surface of a pinnule of the sporophyte of the Wall-rue Spleenwort (*Asplenium Ruta-muraria*) showing the linear aggregations of sporangia (sori), with lateral indusia. [8] A young prothallium arising from a spore; the spore is below. [6] natural size; [1] × 8; [2], [3], and [4] × 350; [5] × 6; [7] × 3; [8] × 240.

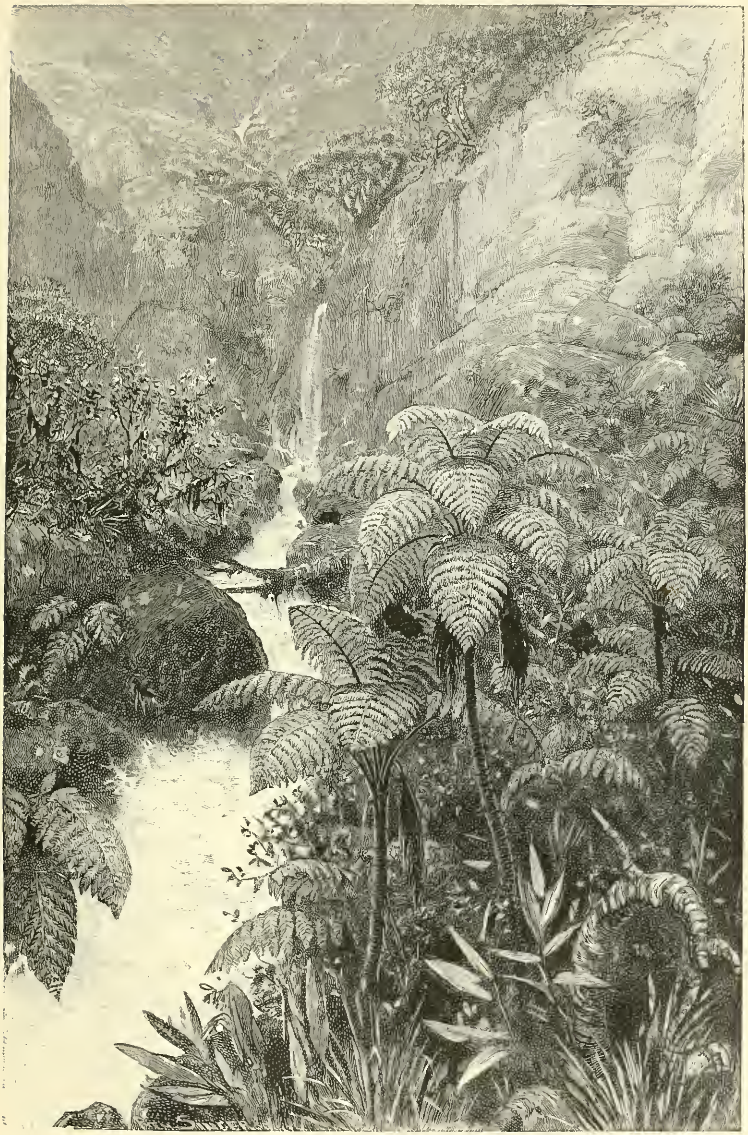

Fig. 347.—Tree-ferns (*Alsophila*) in Ceylon (drawn from nature by Ransonnet).

The impulse to the production of flowering-shoots cannot entirely depend on the prevailing climatic conditions of the year in which the flowering takes place. For in the autumn of the previous year the bud is already laid down, and one can tell by dissecting it whether it will form a flowering or a foliage-shoot. In associating climatic conditions with flower-production, it is the summer of the year previous to flowering which must be taken into account. This is well illustrated by the seasons of the years 1893 and 1894. The summer of 1893 was, as is well known, remarkable for its warmth and long-continued sunshine. This was followed in 1894 (to take an example to hand) by the flowering of many plants in Kew Gardens which are hardly ever known to flower there in the open, under ordinary circumstances. Of these it will be sufficient to mention two Gymnosperms, *Ephedra* and the Maidenhair tree (*Gingko biloba*).

It is easy to observe the fact that in a big tree, of which one side is in the full sun whilst the other is shaded, the shady side produces foliage-shoots for the most part, whilst the sunny side blossoms freely. Nor can one resist the conclusion that it is the sunshine which stimulates the flowering. The same thing is shown by plants, which, growing in dense forest shade, remain without flowers from year to year: but as soon as the trees about them are felled, and the light gains entrance, form flower-buds, and ultimately blossoms and fruits. The advantages accruing to the plant by this change in its surroundings have already been indicated on pp. 394 and 459; but what immediate influence the sunlight has on the building capacity of the plant, and how it is that the tissue which, in the shade forms a foliage-bud should in the sunshine form a flowering shoot, must for the present remain unanswered.

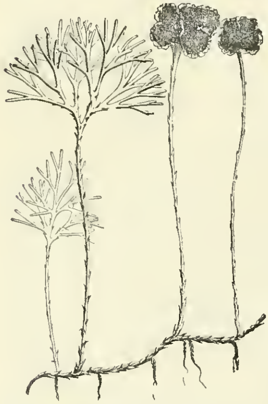

Fig. 348.—*Rhipidopteris peltata* showing sterile fronds to the left, and fertile ones to the right.

And now, as regards *Alternation of Generations*. The relations between the sexual and asexual generations are very various in different portions of the vegetable kingdom. In some groups of plants the two generations are obvious and distinct, in others it is very difficult to draw the line between them. In the Ferns, Horsetails, and Vascular Cryptogams generally, the two generations are quite distinct and easily recognizable. In the Ferns the generation which bears the sexual organs (= sexual generation or oophyte) takes the form of a small, expanded plate of cells, from the under side of which delicate hair-like rhizoids are developed which penetrate the soil (see fig. 189[16], p. 11, and fig. 346[1]). This plate-like structure is usually known as the *prothallium*; it is either heart-shaped or ribbon-like and lobed, attaining a length of from ·5 to 1 centimetre. The sexual organs are borne on the under surface of the prothallium; the antheridia as little hair-like structures distributed over the surface (fig. 346 [3]), the archegonia, flask-like in form, and having the expanded ventral portion sunk in the substance of the prothallium and the neck projecting (see fig. 346 [2]). In the majority of Ferns both sorts of sexual organ occur on the same prothallium, the archegonia on the central parts and in the region of the notch or sinus, the antheridia towards the margin and on the lobes. Fertilization is brought about by the escape of spirally twisted spermatozoids from the antheridia (fig. 346 [4]), which enter the neck of the archegonium, one of them fusing with the egg-cell contained in the ventral portion of that organ (fig. 346 [2]). We may regard the fertilized archegonium as the fruit. It does not become detached from the prothallium, but the fertilized egg-cell develops *in situ* into the next (or asexual) generation, which differs altogether from the sexual one. The egg-cell divides into several cells, one of which gives rise to the young stem, another to the first frond, a third to the primary root, whilst a fourth forms a sucker or "foot", which maintains communication for some time with the tissues of the prothallium (*cf.* fig. 346 [5]). Soon after the first simple frond is expanded, a second is formed, and the young fern-plant is now able to continue its development independent of the prothallium. The prothallium now dies away, and in its place

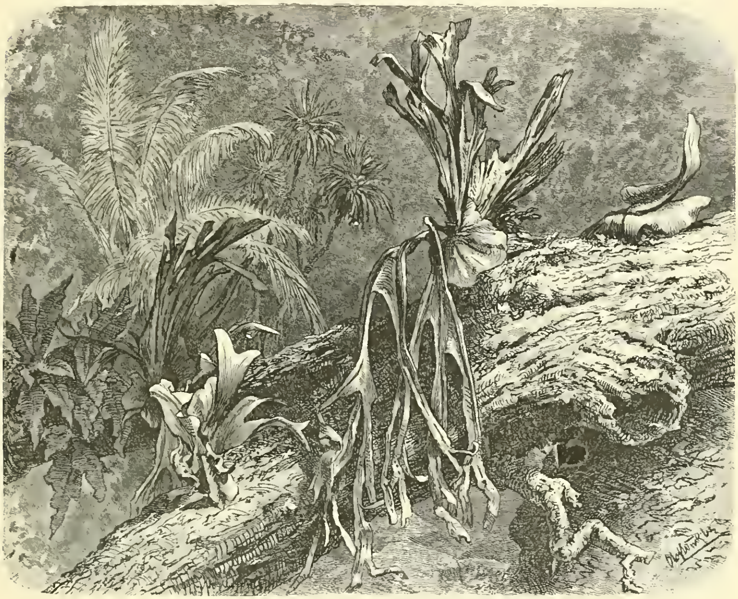

Fig. 349.—*Platycerium alcicorne* (drawn from nature by Selleny).

we have the young fern-plant with its fronds (*cf.* fig. 346 [6]). The fern-plant bears no sexual organs, and must be regarded as the asexual generation (or sporophyte). Its first fronds provide the necessary food-materials for the production of new fronds, which arise in increasing numbers from the stem-apex; as a rule the stem remains short, or it may be elongated horizontally as a rhizome, or, in the Tree Ferns (*cf.* fig. 347), it develops into an erect caudex bearing a tuft of green fronds at its apex. In addition to their purely assimilating function, the fronds are concerned in the propagation of the plant, and produce quantities of spore-cases (or sporangia) containing spores. These sporangia arise in clusters, known as sori, and are usually situated on the under sides of the fronds (see figs. 346 [6] and 346 [7], and fig. 189, p. 11). In the majority of Ferns these two functions—assimilation and spore-production—are performed by one and the same frond, and there is no especial difference in structure between the assimilating and spore-producing portions. But in the so-called "Flowering Fern", or Royal Fern (*Osmunda regalis*), these two portions of the frond stand out in marked contrast; the topmost pinnules of the frond are entirely covered with sporangia, and light brown in colour, whilst the lower portions are bright green, and quite destitute of sporangia. In the Hard Fern (*Blechnum Spicant*) and Parsley Fern (*Allosorus crispus*) there is a distinction between the sterile and fertile fronds, the pinnules of fronds which bear sporangia being much narrower than those of purely assimilating fronds. In *Rhipidopteris peltata*, again, the fertile fronds are disc-like, whilst the assimilating fronds are branched and filamentous (see fig. 348); in *Platycerium alcicorne* the fertile fronds are branched like a reindeer horn, whilst the sterile ones form great green discs in close contact with the bark of the tree on which it grows, and remind one of huge prothallia (see fig. 349). As soon as the spores are mature they are discharged from the sporangia and scattered by the wind. Falling on moist earth, on the bark of a tree, or in a rocky cleft, they germinate, producing prothallia, upon which the sexual organs are borne (*cf.* fig. 346 [8]). Thus in the Fern, two stages are well shown in the life-cycle, (1) the prothallium, the sexual generation or oophyte, and (2) the fern-plant, the asexual generation (or sporophyte), which bears spores, these in turn give rise to the first generation again.

In the Horsetails (Equisetaceæ), which have been figured and referred to at p. 14, a similar alternation of generations occurs. The fern itself is the asexual generation, and bears cones of sporangium-producing scales. From the contained spores prothallia are formed. In several species of Horsetail (e.g. *Equisetum sylvaticum*, fig. 190 [7], p. 14) one and the same shoot bears the organs of assimilation and spore-production; whilst in other species (e.g. *Equisetum arvense*) these functions are relegated to distinct shoots; *i.e.* shoots formed in spring, which terminate in cones (fig. 190 [2], p. 14), and others formed later, which bear numerous green assimilating branches, but no cones (fig. 190 [1], p. 14).

In the group of the Lycopodinæ very interesting conditions prevail. In the so-called Club Mosses (Lycopodiaceæ) the plant is much branched, and in a great many species of *Lycopodium* (e.g. *Lycopodium annotinum*, fig. 378) the shoots end in cones of closely-fitting scales, each of which bears a sporangium. The spores in *Lycopodium* are all alike, and on germination form prothallia, which bear antheridia and archegonia. It is interesting to note in passing that we have only become acquainted with these prothallia in recent years, and for the most part in exotic species. The prothallia of a limited number of European species, however, have been seen. Included in the Lycopodinæ is the genus *Selaginella* (*cf.* fig. 111[1], vol. i. p. 421), resembling *Lycopodium* in its moss-like habit, but differing from it in that *two sorts of spores* are produced. These spores, known as *macrospores* and *microspores*, arise in different sporangia in the same cone, in many cases. The macrospores are relatively large, and are contained four in a sporangium; the microspores are small, and a large number of them is present in a sporangium. The prothallia resulting from their germination are of two kinds; the macrospore gives rise to a female prothallium which bears archegonia; the microspore to a much reduced male prothallium bearing a single antheridium. The sexual generation—which in the Fern consists of *one structure*, the prothallium—here consists of *two structures*, the male and female prothallia. After fertilization the archegonium gives rise to a new, asexual *Selaginella* plant.

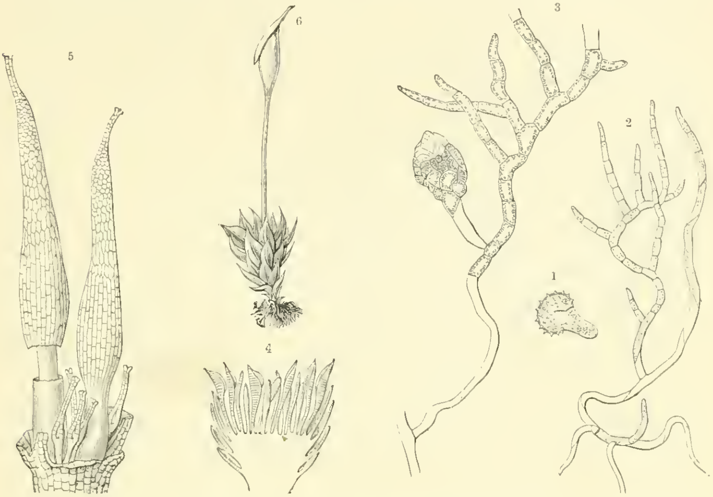

Fig. 350.—Alternation of Generations in Mosses.

[1] A spore germinating. [2] A moss-protonema. [3] Protonema giving rise to a bud from which will arise a leafy moss-shoot [4] Longitudinal section of tip of a male shoot of a moss-plant; antheridia are present between the scales. [5] Tip of a female shoot with archegonia; two of them have much enlarged due to the swelling of the young sporogoniums within. [6] Leafy female shoot of a moss-plant with fully developed sporogonium at its tip. Spores arise asexually in the terminal capsule. [1, 2, 3] × 350–400; [4] × 15; [5] × 80; [6] × 5.

This differentiation amongst the spores in *Selaginella* (in consequence of which the plant is termed *heterosporous*, in contradistinction to Ferns, and *Lycopodium*, which, having one sort of spore only, are termed *homosporous*) is of interest, since it leads on to the condition prevailing in Flowering Plants. In these the alternation of generations is not obvious, no recognizable and detached sexual generations being seen. But on certain shoots of flowering plants (*i.e.* in the flowers) sporangium-bearing leaves are borne; these are the stamens and carpels respectively. The sporangium borne by the stamen is the pollen-sac, and the contained pollen-grains are the microspores. The microspore or pollen-grain, when it germinates on the stigma (or in the micropyle, in Conifers, *cf.* p. 418) forms a pollen-tube, which contains the male fertilizing element, corresponding to a spermatozoid. Of course the conditions of fertilization in the Flowering Plant are altogether different from those obtaining in the Vascular Crytogams, and motile swimming spermatozoids are no longer produced. The sporangium borne by the carpel, on the other hand, is the ovule, and the embryo-sac contained within the ovule is regarded as the macrospore. As a rule but one macrospore is met with, but in certain Amentaceæ (e.g. *Carpinus*, see fig. 314A, p. 412) more embryo-sacs (macrospores) than one are present. In the Flowering Plant the macrospore is not shed from its sporangium (ovule), but germinates *in situ*, forming an egg-apparatus (*cf.* fig. 316 and p. 417), and certain other cells, which ultimately form the endosperm. These structures are regarded respectively as corresponding to the archegonium and female prothallium of such a heterosporous Vascular Cryptogam as *Selaginella*. If the contents of the embryo-sac in Gymnosperms (see p. 415) and in Angiosperms (see p. 417), respectively, are compared with the female prothallium of *Selaginella* or other heterosporous Vascular Cryptogam, it will be seen that the Gymnosperm shows the greater agreement. In it the archegonia are still quite recognizable as such, though these now take part in quite a different type of fertilization. In all Flowering Plants (Gymnosperms and Angiosperms) as opposed to the Vascular Cryptogams, the microspores produce pollen-tubes in the vicinity of the ovules, and these penetrate to the embryo-sac (macrospore) and fertilize the egg-cell. Consequently the counterpart of the archegonium is not exposed, as it is in Vascular Cryptogams, in which a free-swimming spermatozoid has to gain entrance.

Thus we see that in Flowering Plants the female prothallium or sexual generation is hidden away in the embryo-sac, and is never an independent structure. This fact is correlated with the different manner of fertilization which obtains in Flowering Plants as compared with Vascular Cryptogams.

In the Mosses the sexual organs are formed at the tips of little leafy shoots; fertilization is much as in Ferns, and from the fertilized egg a new (asexual) generation arises. This generation, known in Mosses as the sporogonium, consists of a stalk (the seta) terminating in a spore-capsule above. The sporogonium develops within the archegonium on the sexual generation of the Moss. The base of the seta penetrates some distance into the fertile Moss-shoot, and is in this way able to absorb nourishment. As the sporogonium elongates, the archegonial wall stretches with it up to a certain point, then it breaks across transversely and the upper portion is raised up on the capsule as a sort of hood or extinguisher (the *calyptra*, see figs. 350^5 and 350^6). Ultimately this hood is thrown off and the capsule, within which quantities of spores are produced, opens. The spores are readily distributed by the wind shaking the capsule on its stalk. It should be noted that in Mosses this asexual generation (the sporogonium) never becomes independent of the sexual Moss-plant; the base of its stalk always remains embedded in the tissues of the sexual generation. In the Ferns, on the other hand, the asexual generation (= the Fern-plant), though at first drawing nutriment from the prothallium (*cf.* p. 475) by its "foot", soon becomes quite independent, the prothallium dying away. The form of the sporogonium is very varied in different groups of Mosses. In fig. 351 are shown the sporogonia of a number of Mosses, including species of *Splachnum* (*S. luteum, S. vasculosum,* and *S. ampullaceum*), a rare form occurring on the excrements of cattle, reindeer, &c., that of the already-mentioned Luminous Moss (*Schistostega osmundacea, cf.* vol. i. p. 385); and in fig. 191, p. 16

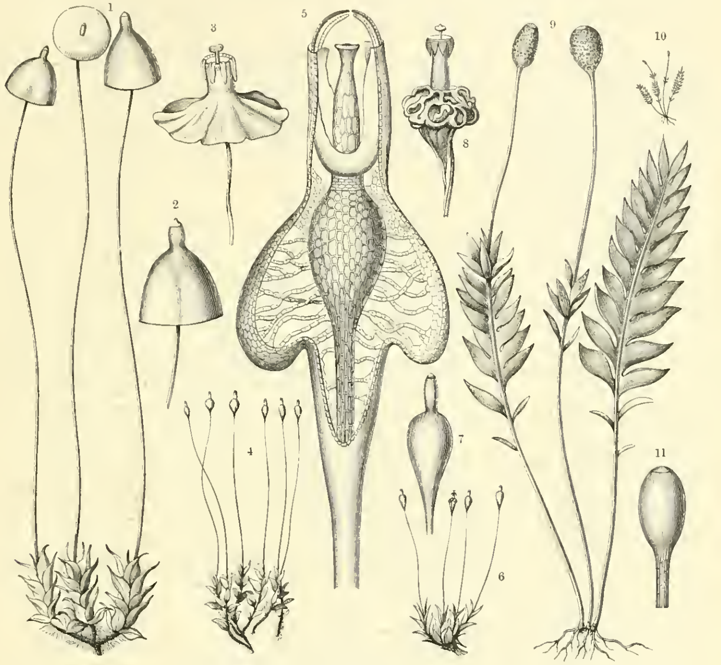

Fig. 351.—Alternation of Generations in Mosses. Various forms of sporogonium, which as the asexual generation have been produced at the tips of leafy shoots.

^{1} *Splachnum luteum.* ^{2} An unripe capsule of the same. ^{3} A ripe and open capsule of the same. ^{4} *Splachnum vasculosum.* ^{5} Longitudinal section of a ripe capsule of this Moss. ^{6} *Splachnum ampullaceum.* ^{7} An unripe capsule. ^{8} A ripe capsule of the same. ^{9} and ^{10} *Schistostega osmundacea.* ^{11} A ripe capsule of the same. $^{1, 4, 6, 10}$ natural size; $^{2, 3}$ × 2; $^{7, 8, 9}$ × 10; ^{11} × 15; ^{5} × 100.

those of *Polytrichum, Bryum, Hylocomium, Andreæa,* and *Sphagnum.* The spores of the asexual generation germinate on a moist substratum, giving rise to a tubular filament which becomes segmented, and gives rise to a considerable growth of simple character, known as the *protonema* (see fig. 350 [2]). Certain rows of cells of the protonema are colourless and penetrate the ground as rhizoids, the others are extended on the soil and are bright green in colour. After a while bud-like structures arise here and there upon the protonema (see fig. 350 [3]); these develop into leafy Moss-shoots, upon which the sexual organs are borne—usually in little clusters. Thus in Mosses, the sexual generation has two stages; the protonema and the leafy Moss-plant. From the latter arises the asexual generation or sporogonium. In many of the Liverworts the sexual generation is much simpler, consisting of a thallus, in which the archegonia and antheridia are sunk. However, a great variety is met with amongst them, but the main relations of the sexual and asexual generations are much as in Mosses.

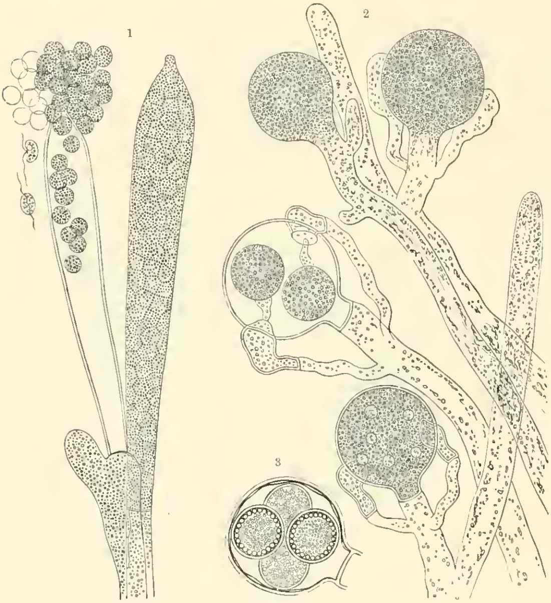

Fig. 352.—Asexual and sexual reproduction in Saprolegniaceæ.

[1] Formation of asexual zoospores in *Achlya.* [2] Oogonia with antheridia and fertilizing tubes. [3] Fruit. All figures × 300. (After Sachs.)

It will be noted that in Mosses the sexual generation is much more complex a structure than the corresponding structure (the prothallium) in Ferns. The asexual generation, on the other hand, in Mosses is never independent, whilst in Ferns it becomes so quite soon and attains, in the latter group, to much greater structural complexity than in the Mosses.

Amongst the large assemblage of simple plants which together constitute the class Thallophyta we find in some forms an incipient alternation of generations on the lines already described for Mosses, Ferns, &c.; in others there is no suggestion of such alternation; and in others again (such forms are numerous), an alternation occurs, but of a character quite different from that of higher plants.

First we will mention such as show an alternation of generations not unlike that of the Fern. It will be remembered that in the Fern there is a simple prothallium upon which the sexual organs arise, and from the fertilized egg-cell a new generation, of considerable dimensions, is developed which produces asexual spores, these in turn giving rise to prothallia. In the group of the Red Seaweeds or Florideæ (*cf.* pp. 61, 62, and figs. 204^7 and 204^9, p. 53), the seaweed plant is the sexual generation and bears the rudimentary fruits with trichogynes and the male spermatia. After fertilization, a considerable growth is initiated, which results in a mass of spores being abstricted, these spores being in many cases inclosed in a sort of capsule, which develops concurrently with the spores. This capsular structure with its spores we may interpret as a very simple asexual generation comparable to the sporogonium of a Moss or to a Fern-plant with its spores. Of course this asexual generation is very ill-marked in the Red Seaweed, and it is difficult to quite draw the line between it and the sexual generation of which it forms a continuation. It has this in common with Mosses and Ferns; that from a single process of fertilization a numerous progeny of spores is begotten—spores which on germinating give rise to sexual plants again.

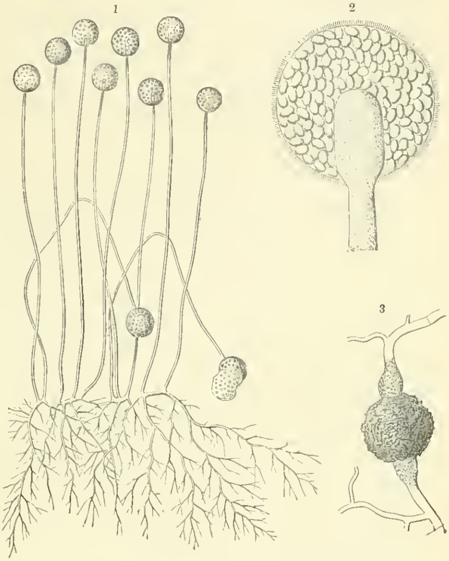

Fig. 353.—Asexual and sexual reproduction in the Mucorini.

1 Mycelium producing asexual spores in stalked sporangia. 2 A single sporangium in section. 3 Formation of a zygospore. 1 × 40; 2 × 260; 3 × 180.

The brown Wrack, *Fucus,* is an example of a Thallophyte in which alternation of generations is not known to take place. In this seaweed every generation is a sexual generation, and the fertilized egg-cells, so far as is known, give rise—not to spores—but to new sexual generations. Its life-history is described and figured on pp. 51, 52.

And now we come to a type of alternation of generations, prevalent amongst green Algæ and some families of Fungi, which seems to be quite distinct from the rhythmic alternation which obtains in the Mosses, Ferns, &c. The oft-mentioned tubular Alga, *Vaucheria sessilis* (belonging to the family of the Siphonaceæ) will serve as an admirable example of what we mean. This plant reproduces sexually (*cf.* pp. 57, 58, and figs. 204^5 and 204^6, p. 53) by means of oogonia and antheridia of simple character; it also propagates itself by means of large asexual zoospores which it liberates from the tips of its tubular filaments (*cf.* vol. i. pp. 23, 24, and Plate I., figs. *a–d*). But these two classes of reproduction do not occur simultaneously upon one and the same plant; but rather, so it was till lately supposed, upon generations which alternated with one another either regularly or irregularly. Sometimes the *Vaucheria*-plant arising from a zoospore bore sexual organs, and from the fertilized egg-cell arose a non-sexual plant which gave rise to zoospores again; or a series of asexual generations followed one another, the series being terminated by a sexual generation, the fertilized egg-cells of which entered on a resting stage.

The meaning of this supposed alternation of generations in *Vaucheria* has recently been cleared up by Klebs in a series of very interesting culture-experiments. Without describing these in detail we may briefly indicate some of Klebs's results. If a number of young *Vaucheria*-plants be cultivated, three possibilities are open; the plants may produce sexual organs; they may be reproduced asexually by zoospores; or, finally, they may remain perfectly sterile. Klebs found that by appropriate treatment of plants, he could bring about any of these possibilities at will. Young plants placed in a 2–4 per cent sugar solution, and kept in the light at a temperature not falling below 3° C., invariably produced sexual organs in the course of some ten days. Other plants, which had been grown in a dilute nutrient solution of food-salts in the light for a short time, were removed to water and placed in the dark. These plants soon gave rise to enormous quantities of zoospores; in time these zoospores germinated, and the resulting plants in their turn produced fresh zoospores, and so on. The third condition, that of sterility, was obtained by keeping plants in strong sugar solution (10 per cent), and also by other methods. More than this, the same plants were caused to alter their mode of reproduction by varying the conditions; in this way it was possible to cause them at one time to produce zoospores and at another sexual organs. This brief summary is sufficient to show that a given *Vaucheria*-plant has no inherent tendency to reproduce asexually in preference to sexually, or conversely; and that its manner of reproduction (or its abstention from reproduction) depends on the conditions which prevail outside the plant. Thus, in *Vaucheria*, no true alternation of generations prevails in the sense in which it does in Mosses and Ferns, and every generation is potentially both a sexual and an asexual generation. It is the external conditions which call forth the one or the other.

In a great many other Thallophytes the same is no doubt true, though exact experiments have yet to be performed on the majority of them. We know it to be so in *Botrydium* and in the Water-net (*Hydrodictyon*) and in others. The Water-net (figured on p. 24) propagates asexually by the contents of its cells breaking up into very numerous (7000–20,000) swarm-spores (thallidia) which

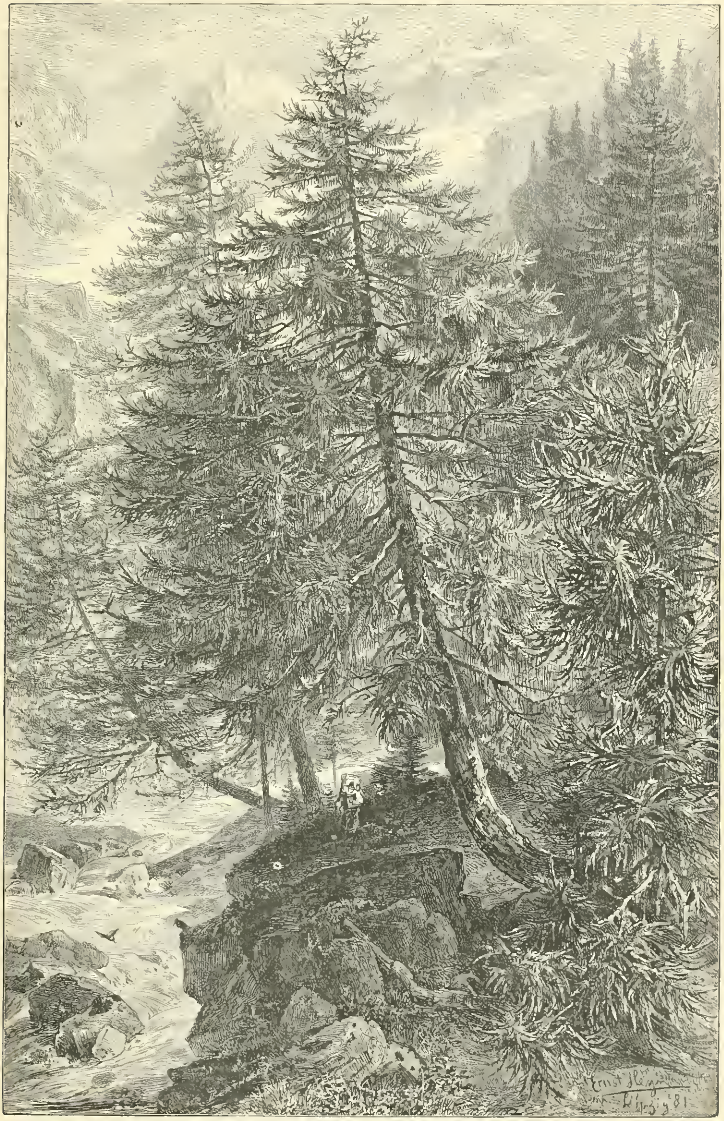

Fig. 354.—Larch-trees (*Larix europæa*).

do not forthwith escape, but swim about for a while within the wall of the cell in which they originate. Then they join together into a tiny net which escapes, ultimately growing to its full size (*cf.* vol. i. p. 36). In sexual reproduction a much larger number (30,000–100,000) of small motile bodies (gametes) escape and conjugate in pairs. Klebs has found here also that either of these methods can be produced at will by altering the conditions under which the plant grows.

Among the Fungi the Saprolegniaceæ show well-marked sexual and asexual methods of propagation. These are mould-like forms which attack fish and other aquatic animals upon which they are parasitic. Purely asexual reproduction occurs by means of zoospores which are liberated from long, club-shaped sporangia (fig. 352^1); whilst sexual reproduction (which may occur upon the same plant) takes place by spherical oogonia arising upon certain branches and antheridia as small lateral twigs below them (fig. 352^2). The latter perforate the oogonium-wall with their "fertilizing tubes" (*cf.* the allied *Pythium*, p. 56), but curiously enough there is no real fertilization. Nothing has been observed to pass from the fertilizing-tubes to the egg-cells, and we must regard the process of fertilization here as obsolete. The egg-cells, though unfertilized, put on cell-walls (fig. 352^3) and germinate, as one might say, parthenogenetically.

In the Moulds of the family Mucorini the mycelium establishes itself upon an organic substratum and produces, at one time, long-stalked sporangia (figs. 353^1 and 353^2), and at another short sac-like outgrowths which arise in pairs near one another and conjugate, forming a zygospore (fig. 353^3). Whether this or that method of reproduction prevails in these Fungi depends, most probably, on external conditions; indeed examples from amongst the Fungi could be adduced in which careful experiment has determined that this is the case.

In conclusion we may inquire how is it that alternation of generations is so widely distributed amongst plants, whilst in the animal kingdom it is of relatively rare occurrence. We obtain an answer to this question when we consider what are the distinguishing characters of those animals in which alternation of generations takes place. The corals, polyps, and other animals exhibiting alternation are in great part sessile organisms, attached to their substratum. But when a fixed organism propagates itself and distributes its kind, it must commit portions of itself to the winds or to currents of water, if new regions are to be occupied; a condition applying equally to plants and animals. Or, as an alternative, sexually-produced progeny may be liberated from the mother-organism and take up new positions. But sexual reproduction amongst fixed organisms requires rather special arrangements, and even with their aid is not invariably certain. Interference with fertilization may connote the extinction of the species; consequently a propagation by asexual means is of great importance for such organisms. By a definite alternation of the two methods, by a single act of fertilizing leading to an organism capable of multiplying itself almost indefinitely by asexual spores, a numerous progeny is ensured even from a single sexual union. Take the case of the Fern-prothallium; from one fertilized archegonium arises a Fern-plant with many fronds and capable of producing millions of spores. Thus the species, whilst retaining to itself such advantages as may be inherent in the sexual process, is likewise able to diffuse itself in large numbers over an extended area by means of its numerous asexually-produced spores.

Allusion has been made to the advantages inherent in the sexual process. The investigation of their precise nature will be one of the main problems reserved for the second part of this volume. That a production of flowers and a ripening of seed is not *absolutely essential* for the maintenance and distribution of plants, seems not improbable—judging from the considerable number of plants which do well and flourish without them.

THE HISTORY OF SPECIES.

1. THE NATURE OF SPECIES.

Definition of Species—Specific Constitution of Protoplasm.

DEFINITION OF SPECIES.

The history of plant species is founded on the history of individual plants given in the first section of this volume, more particularly on the results afforded by investigation into the processes of reproduction and propagation. It deals with the description of the species from its origin to its end, and also takes cognizance of the replacing of extinct species by new ones. The execution of this task is less easy than the representation of the life-history of the individual which can be deduced from direct observation and experience. It being possible to follow the course of even long-lived individuals, beginning with the origin of the embryo and following it through all its life's stages, the meaning of certain vital processes as, for example, the pollination of the stigmas and the germination of the seeds can be understood. The origin of most of our present species, however, which have arisen without the aid of man, is shrouded in mystery; it occurred in long past ages and we are obliged to fall back on conjectures which, however intelligent and however they may be supported by carefully weighed considerations, are still only conjectures after all. For purposes of direct observation we have only the fossil remains of earlier times and the species which are living at the present day. By comparing these with one another, and by inferring the nature of extinct forms from that of living species, we are able to construct a chain of conclusions which after all may be regarded as the best available substitute for a history of species.

The most important foundations for these conclusions are afforded by the knowledge of the relations of living species to their environment, especially the recognition of those causes which bring about permanent changes of form, for this alone can elucidate the question of the origin of new species. Before discussing these important questions the nature of species must be described and we must understand exactly what is meant by a species.

The definition of a species was first introduced into science by Linnæus, and the Latin word "species" owes its origin in this sense to the great master of Botany. Linnæus laid down that each species consists of similar individuals which are related together by their origin, and which are the unaltered descendants of a common ancestor or pair of ancestors. It does not affect the value of the definition that Linnæus considered these ancestors to be creations of the "*infinitum ens*"; but it is very important that he recognized existing organisms as the continuation, the rejuvenated portions of one and the same living being, so that the species is not a figment of the human mind, but is something which actually has an objective existence.

Moreover, to decide which individuals are similar, *i.e.* of the same species, we take note of characters apparent to our senses, especially of the form and structure of the plant-body. Each species has its special features or characteristics, and all individuals possessing these specific marks are said to belong to the same species. Specific characteristics are hereditary, and are transmitted unaltered to the descendants. There are, however, some plant characteristics which are not inherited, but which may appear or not according as the individual develops in this or that place, and these must be regarded as the expression of certain external conditions which have an influence on plant-organization. They form the foundation for the existence of the variety, according to Linnæus. The individuals of each species may vary, but the variations are not handed down to posterity; they change according to position and other external influences. Systematic Botanists since the time of Linnæus have therefore to consider two kinds of distinguishing marks or characteristics: (1) those which are inconstant and not inherited; and (2) those which are constant under widely different external conditions and are hereditary. The latter determine the species, the former the variety. Each species may exhibit several varieties at one time, but its specific characteristics remain unaltered. If the specific marks should have undergone any alteration in the descendants, these will form a new species, or rather the appearance of an individual furnished with new specific marks forms the starting-point for a new species.

The relations of outward form and structure relied on by systematic Botanists in the identification of plant species depend of course on the plan of construction of the protoplasm of the species in question, and again only the specific constitution of the protoplasm determines this constructive plan. Before we can arrive at a correct idea of the nature of species, therefore, it is above all things necessary to obtain as clear a picture as possible of the relations of the protoplasm to the external visible form.

THE SPECIFIC CONSTITUTION OF PROTOPLASM.

Mention has previously been made of the remarkable fact that the species of a genus differing from one another in outward appearance also differ in respect of the scents secreted by them. Many Roses have different scents (*Rosa alpina, arvensis, cinnamomea, Gallica, Indica, Nasterana, pomifera, rubiginosa, sepium,* &c.), and a blind man could distinguish each species by the scent of its flowers. This is also true of species the foliage, stem, and roots of which emit odorous substances. By rubbing the foliage of different species of Thyme in one's fingers

(*Thymus Chamædrys, montanus, vulgaris, Zygis,* &c.), each will give off a peculiar scent; and when the roots or root-stocks of different Valerians (*Valeriana celtica, dioica, elongata, officinalis, Phu, saxatilis,* &c.), or of different species of the Asarabacca genus (*Asarum Canadense, Europæum,* &c.) are dug up, though they all smell of valerianic acid or spikenard, each species has in addition a distinctive odour of its own. The edible Fungi (*Polyporus confluens, frondosus, ovinus,* &c.), Garlics (*Allium ascalonicum, Cepa, Porrum, sativum, Schœnoprasum,* &c.), various Currants (*Ribes alpinum, petræum, rubrum,* &c.), and the Strawberries (*Fragaria collina, elatior, grandiflora, vesca,* &c.) all demonstrate most decisively that our olfactory nerves can distinguish between the different species of some genera. It might also be pointed out that it is no infrequent occurrence for one species of a genus to be poisonous to man while another is harmless, *e.g.* species of the Star-Anise genus (*Illicium anisatum* and *religiosum*), and of the fungal genus Lactarius (*Lactarius deliciosus* and *torminosus*). It is familiar to naturalists how precisely herbivorous animals can distinguish between different species of plants. The caterpillar of the Oleander Hawk-moth (*Sphinx Nerii*) lives exclusively on the Oleander (*Nerium Oleander*), that of a small Mediterranean butterfly, *Thais Hypermnestra,* only on the Birthwort (*Aristolochia Clematitis*), that of the small Tortoise-shell Butterfly (*Vanessa Urticæ*) only on the leaves of the large Stinging Nettle, and that of *Libythea Celtis* only on the foliage of the Nettle-tree (*Celtis australis*). Each caterpillar can at once distinguish the only species which suits it from numerous other similar ones. A friend of mine once found the caterpillar of a butterfly he did not know high up on the Gletscherstock in the Stubai, Tyrol, which he took into the valley with him intending to feed it until it became a chrysalis in order to obtain the butterfly. In the valley he placed it on about a hundred different plants in the hope that it would settle on one or other and use it as food. But it would not touch one of them, although caterpillars apparently suffer from voracious appetites. My friend now determined to revisit the spot where he had found the caterpillar and to set it at liberty there. When he did so it at once crawled as quickly as possible to a certain plant (*Cardamine alpina*) and attacked it with great eagerness. Later he discovered it to be the caterpillar of *Pieris Callidice,* which only feeds on the small Alpine Bitter-cress (*Cardamine alpina*). Generalizing from these instances, many more of which might be given, we are justified in assuming that the aromatic substances, alkaloids, acids, &c., which are manufactured in the plant metabolism are quite definite for each particular species. But it is equally obvious that a specific protoplasm is necessary for the manufacture of specific substances, or, in other words, that each plant-species with a certain definite form possesses also a definitely constituted protoplasm of its own.

The behaviour of different species with regard to temperature is especially worthy of note among the many observations which support this view. It is well known that seeds of various species which closely resemble one another in outward appearance differ greatly in the temperature they require for germination. Seeds of one species are content with a low temperature, while those of another require much greater heat, although the eye can distinguish no difference in the structure of their coat, in their manner of storing reserve food, or in the structure of their embryos. The same may be said of the freezing of plants. Many Californian and Mexican Pines (*Pinus*) are very like those of Northern and Central Europe, and yet the one will be frozen to death as soon as the temperature sinks below freezing point, while the other can sustain winter temperatures of −20° C. without injury. There seems to be no reason why the South European Junipers, *Juniperus Oxycedrus* and *phœnicea,* which are apparently of the same structure as the similar species *Juniperus nana* and *Sabina,* should not flourish equally well on our mountain heights in the Central Alps, where the latter cover whole mountain peaks and send their roots into ground which is covered with snow eight months every year, and is frozen hard for months together. The common Ivy (*Hedera Helix*) grows in Central Europe without any protection from the fairly severe cold of winter; the S. European Ivy, *Hedera poetarum,* which is very similar to the common species, but can be distinguished from it by several external characteristics, requires a protecting roof in the gardens of Central Europe if it is to survive the winter unkilled by the frost. The same is true of two closely allied species of Marigold, viz. *Calendula arvensis* and *fulgida,* the former growing in Central, the latter in Southern Europe. In 1874 I sowed seeds of *Calendula arvensis* from the Rhine district side by side in the same garden-bed with seeds of *Calendula fulgida,* which had been gathered in Sicily. Very luxuriant plants which flowered in profusion grew up from both kinds of seeds. The first frost in that year in the place where the experiment was made occurred on October 25th. *Calendula arvensis* was not injured; its foliage was fresh and green, and remained in this condition during the following days, although, until November 2nd, the temperature fell every night from −1·5° to −2·5° C., and in the morning the stem, leaves, and flowers were studded with hoar-frost. *Calendula fulgida,* on the other hand, was destroyed by the frost on the night of the 24th–25th October. Its leaves and stems withered and turned brown, and exhibited all the symptoms observable in death by freezing. In 1864 I found a *Cytisus* on the rocky shores of the Adriatic Sea at Rovigno, which closely resembled the wide-spread *Cytisus nigricans* of Central Europe, but which had certain distinguishing features. I named it *Cytisus australis.* Some of its seeds were collected, and from them strong young seedlings were obtained in the following year. These were planted in the Botanic Garden at Innsbruck with some seedlings of *Cytisus nigricans* of the same age from the Danube valley, near Mautern, in Lower Austria. Both grew under identical external conditions, and appeared to be equally vigorous. But during the winter the plants of the *Cytisus* from the shores of the Adriatic were killed by the frost, while those of the *Cytisus* from the Danube valley remained healthy and strong. The experiment was repeated with the two plants in the following year. Young plants were again raised from seed, but this time those from the Adriatic coast were protected against the cold, and in this manner they survived the winter without harm. Two years later both the species of *Cytisus* developed flowers and fruits almost simultaneously under the same external conditions, and it was noticed that the same real, if insignificant, deviations were present in the external characteristics which had been present in the parents. This different behaviour of plants which, on account of their form, are described by the Botanist as distinct species, although closely allied, can indeed only be explained by assuming that the protoplasm, though having on the whole a similar constitution, is somewhat different in each species.

As a further confirmation of the assumption that the protoplasm of each species possesses properties which are lacking in that of others, we may take the case of the behaviour of pollen-cells in fertilization. If two kinds of pollen-cells are brought to the stigmas of a plant, *i.e.* pollen-cells of two different species, it usually happens that the one will fertilize the ovules with its pollen-tubes, while the other will be without effect. And yet the conditions are the same in both cases, and the difference in behaviour must therefore depend upon some difference in the protoplasm of the pollen-cells. Protoplasts which swim about as swarm-spores in the same drop of water, exposed to exactly the same condition of light, heat, pressure, &c., display a different behaviour if they belong to a different species. Those of one species will always twist to the right, those of another always to the left, some seek the light, others shun it for the darkest places. But since the protoplasm behaves differently under the influence of the same ray of light, the same temperature, and the same pressure, the cause must be sought for in the tiny mass of protoplasm of which each swarm-spore is composed.

The little amœbæ which proceed from the spores of Myxomycetes are protoplasts without a cell-wall; they live on dead parts of plants, where they feed, grow, divide, and multiply. When the right time comes these amœbæ fuse together to form a body known as a plasmodium, which is ultimately converted into a mass of sporangia (*cf.* vol. i. p. 572). Although the little amœbæ of different species cannot be distinguished from one another, and the plasmodia look like masses of formless protoplasm which only differ sometimes in colour, the resultant sporangial forms exhibit a remarkable variety of forms. From the plasmodium of *Stemonitis fusca* there arises a network of dark brown threads which is penetrated by and borne on a central axis like the shaft of a feather (see figs. 355 [1] and 355 [2]); from that of *Spumaria alba* is formed a white slimy mass resembling the "cuckoo-spit" of the Cicadellidæ and enveloping stem and leaves just in the same way (see fig. 355 [3]); from the plasmodium of *Dictydium cernuum* there arises a globe-like lattice-work, with strong longitudinal ribs and delicate cross-bars, which is carried on a hooked stalk (see figs. 355 [4] and 355 [5]); from the formless plasmodium of *Craterium minutum* arise stalked cups of a gray colour (see figs. 355 [6] and 355 [7]); from that of *Arcyria punicea* short stalked conical bodies not unlike Strawberries (see figs. 355 [8, 9, 10]); the plasmodium of *Lycogala epidendrum*, which penetrates the wood of dead tree-trunks, forms balls of the colour of red-lead, about a centimetre in diameter (see fig. 355 [11]), and out of the plasmodium of *Leocarpus fragilis*, which spreads over dead branches and twigs, proceed stalked egg-shaped sporangia, with little brown coats (see fig. 355[12]). And all these peculiar forms arise under similar external conditions from apparently similar slimy and formless masses of protoplasm.

The same thing occurs in the Mushroom and Toadstool Fungi (Hymenomycetes) which develop in the mould of the forest ground and on the dead bark of tree-trunks. The mycelium is a network of white threads and strands, and neither the form of the colourless elongated cells composing the network nor the protoplasm within the cells afford any indication by which we can judge the species to which the mycelium belongs. But how different are the fructifications proceeding from these apparently identical mycelia. In a part of the forest ground not twenty paces across there grow large specimens of *Boletus edulis* with chestnut-brown hemispherical caps; a little distance off a group of Chantarelles (*Cantharellus cibarius*), with yellow colour like yolk of egg, close by the Fly-agaric (*Agaricus muscarius* or *Amanita muscaria*), with snow-white stipe and crimson cap (*pileus*) spotted with white, and near at hand, from

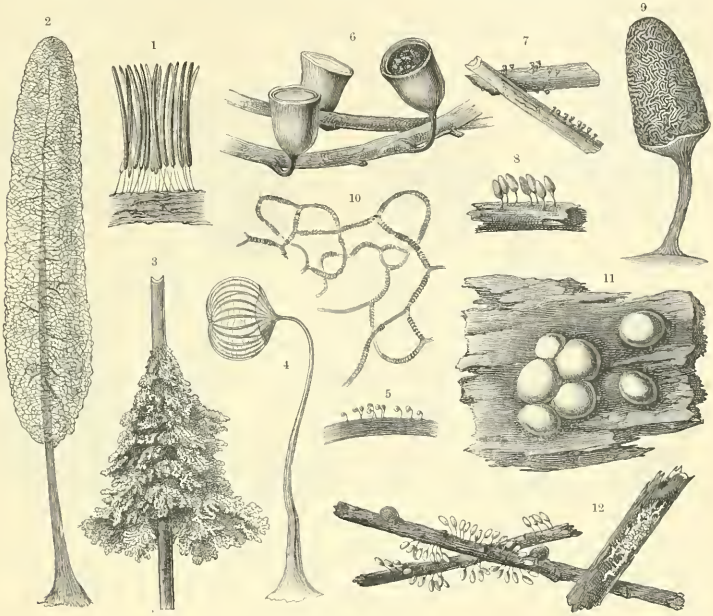

Fig. 355.—Myxomycetes.

1 A group of sporangia of *Stemonitis fusca*. 2 A single sporangium; × 6. 3 Dendritic mass of sporangia of *Spumaria alba* on a Grass leaf. 4 Sporangium of *Dictydium cernuum*; × 25. 5 A group of sporangia of the same. 6 and 7 Sporangia of *Craterium minutum*; 6 × 25. 8 Sporangia of *Arcyria punicea*. 9 A single sporangium; × 10. 10 Part of the net-like capillitium of the same; ×160. 11 Fructification of *Lycogala epidendrum* on a piece of wood. 12 *Leocarpus fragilis*; a plasmodium on the right; several sporangia on the left.

a mycelium which has penetrated the bark and wood of a Beech-tree, grows the horse-shoe-shaped ashen-gray *Polyporus fomentarius* (*cf.* the accompanying Plate XIV., showing these Fungi amid their natural surroundings).

The fruits resulting from the conjugation of the unicellular Desmids are minute balls of protoplasm, and although they may originate from very different species, outwardly there is not the slightest distinction between them. But as soon as these small balls of protoplasm begin to develop, the greatest variety of cell-forms is the result. Each is fashioned after the form of the parent individuals which produced the fruit by conjugating. One cell will be half-moon-shaped, another cylindrical, a third angular and table-shaped, others again stellate and with manifold projections; some have a smooth surface, while the cell-wall of others is beset with spines or studded as if with pearls. The figures above, representing twelve different species of these Desmids, will give some idea of the multiplicity of their forms. And all these varieties spring from apparently identical masses of protoplasm, and develop side by side in the same drop of water, under the same illumination, the same temperature, and, generally speaking, under exactly the same external conditions and stimuli.

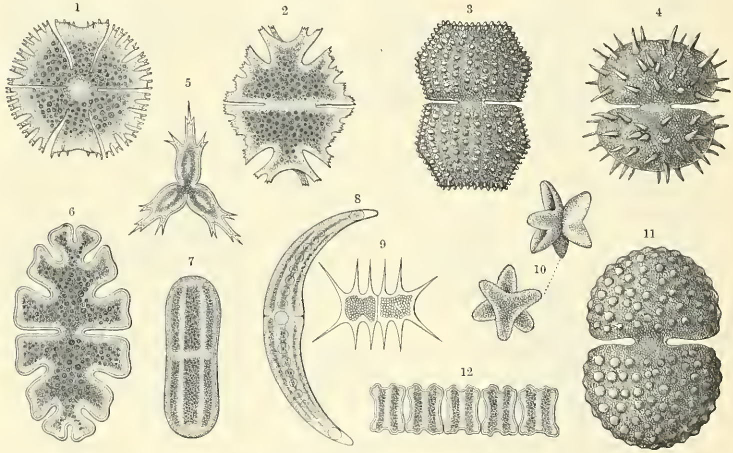

Fig. 356.—Desmidieæ.

[1] *Micrasterias papillifera.* [2] *Micrasterias morsa.* [3] *Cosmarium polygonum.* [4] *Xanthidium aculeatum.* [5] *Staurastrum furcatum.* [6] *Euastrum oblongum.* [7] *Penium Brebissonii.* [6] *Closterium Lunula.* [9] *Xanthidium octocorne.* [10] *Staurastrum alternans* (two views). [11] *Cosmarium tetraophthalmum.* [12] *Aptogonum Desmidium.* All the figures magnified about 200 times.

All these observations and results seem to indicate that the hypothesis as to a specific constitution of the protoplasm in each species is almost a necessary assumption. The word "constitution" has been purposely used instead of "composition", which might be taken to mean essensially the same thing were we

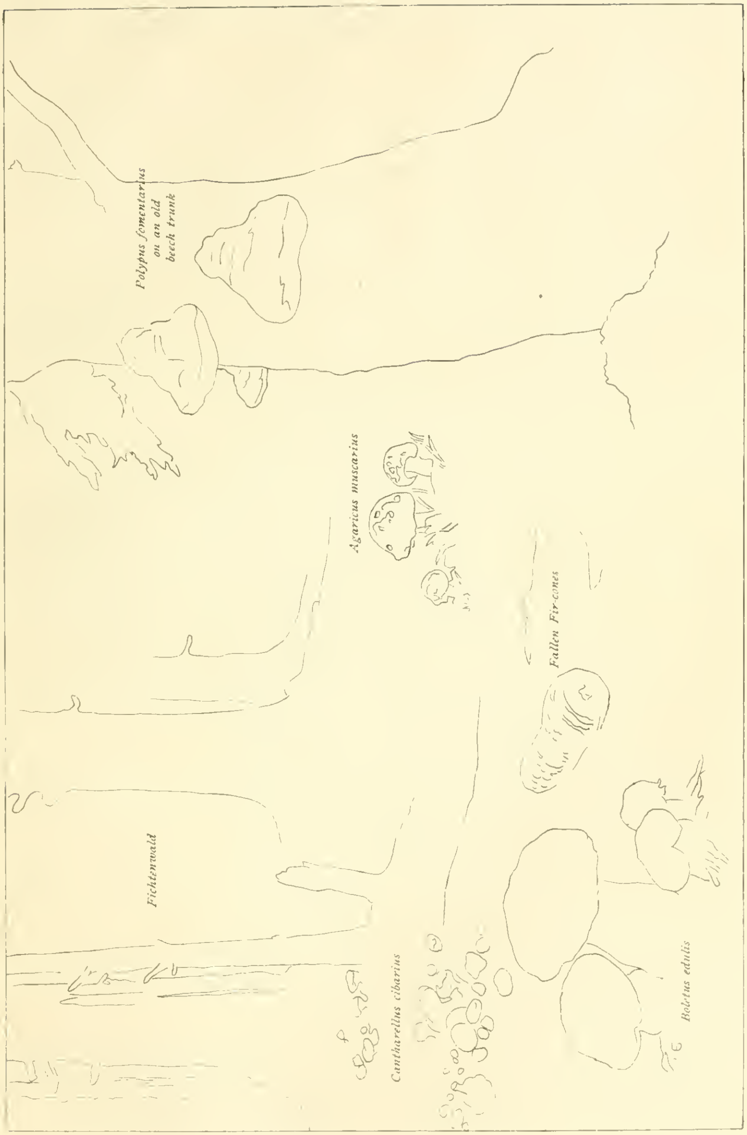
Polypus fomentarius
on an old
beech trunk
Agaricus muscarius
Fallen Fir-cones
Fichtenwald
Cantharellus cibarius
Boletus edulis

PLATE XIV

FUNGI AT HOME.

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dealing merely with a chemical compound. Nothing would be more natural than a comparison with inanimate things whose outwardly perceptible features are the expression of a definite chemical composition, *i.e.* of a certain grouping of molecules and atoms which can be represented by a certain formula. But although this comparison is allowable in general, yet there is an essential difference between mineral and plant species. No formula can be given for the protoplasm of a species of plant, and the structure of a protoplast cannot be compared with that of a crystal. Each protoplast represents an organism which contains very many chemical compounds. It is able to renew them when required, and to modify their grouping as dictated by external stimuli. With these displacements there must of course be a temporary alteration of structure, *i.e.* of the grouping in the formed part of the protoplasm. But all these displacements and alterations take place in each species according to the same plan. The same chemical compounds, the same aromatic bodies, the same acids and the same alkaloids, &c., can alone be demonstrated. The recently-formed parts agree with those already present, and merely fill up the places previously assigned to them. This unalterable law of form which governs the working of the protoplasm in each species is, therefore, dependent on some structure of the protoplasm which is beyond the perception of our senses, and it is this which is termed the *specific constitution of the protoplasm.*

In the above-mentioned Desmids, which afford such especially instructive examples, and in numerous other unicellular plants where all the formative processes are carried on within a single protoplast, it is easy to see the connection between the outward appearance and the specific constitution of the protoplasm. It is more difficult in species where there is greater division of labour, a division into manifold cell-forms and a gradual succession of different members. One might compare the processes occurring in them with similar processes in mineral species, which, with the same chemical composition present a great difference in their outward form and appearance. Carbonate of lime, which forms the mineral species *calcite,* appears in four kinds of crystal-forms, but they all belong to the same system, and can be derived from one another. In the same way the varied cell-forms and tissues, as well as the cotyledons, foliage, and floral-leaves, which arise from the same plant in regular succession, are to be regarded as members of the same system, succeeding one another in definite rule, although the specific constitution of the protoplasm in the particular species undergoes no change.

At one time the idea was prevalent that there are two kinds of protoplasm, *idioplasm* and *cytoplasm.* To the former was assigned the formative activity, while the latter was regarded as merely a nutritive plasm or medium. Subsequently it was shown that in every protoplast there is a more definite part, termed the *nucleus,* which dominates the whole, especially in the building and renewal of the cell-wall, while it also takes a leading part in cell-division and multiplication. Thus the assumption that all formative processes are carried on through the cell-nucleus was held to be correct. The fact of the constancy of species from generation to generation was therefore referred, especially, to the specific constitution of the cell-nucleus. Since the nucleus plays such an important part in the process of fertilization, which precedes the inception of the new individual in sexual reproduction, the hypothesis was put forward that the constancy of form in the offspring, or, in other words, the transmission of form, depends upon the specific constitution of the nuclei taking part in this process. Nor would this hypothesis be open to objection had not recent investigations shown it to be extremely probable that portions of the male cell other than the nucleus assist at this process. If, as it appears, more than the mere nucleus passes over from the pollen-tube at fertilization (*cf.* p. 417), how can we certainly allege that (to take a definite case) all the properties which the young plant inherits from its male parent are transmitted through the medium of the nucleus? If it be true that a certain portion of the cell-protoplasm takes part in this act, it must be proved that it plays only a subordinate part in the process (*e.g.* a nutritive function) before we can attribute to the nucleus the part of sole carrier of transmitted properties.

To the proposition that new individuals with the unaltered properties and characteristics of the species can only spring from the protoplasm of this nucleus, we cannot assent. Thousands of plant-species reproduce asexually in unaltered form by spores and other offshoots. As already stated so often, every young cell of a plant may be the starting-point of an offshoot or brood-body, and so may lead to the beginning of a new individual; and an individual produced in this way bears all the characteristics of the parent plant which produced the offshoot. It might even be asserted that the features of the species are more certainly inherited in the case of reproduction by offshoots and brood-bodies than in sexual reproduction, and in a subsequent chapter it will be shown that it is sexual reproduction alone which affords the possibility of posterity with altered characteristics.

The view that the part surrounding the nucleus of a protoplast, the cell-protoplasm or *cytoplasm*, has no formative importance is not borne out by the evidence of investigations into the origin of the so-called galls, which we shall discuss in detail later, nor by our knowledge of hybrids. On the contrary, hybridization causes not only an alteration of form in the new individual arising from the germ-nucleus, but also an alteration in the form of the tissue in the region of the ovule exclusively influenced by the cytoplasm, so that the effect of hybridization can be recognized even in the fruit which arises from the ovary. Every influence on the cell-nucleus must be transmitted through the cytoplasm. But it would be much more difficult to imagine that the cytoplasm remains quite indifferent to this transference than that it also experiences a change identical with or similar to that undergone by the cell-nucleus. Fortified by these considerations, we may then assume (1) that all protoplasts which we know are able to form the starting-points of new individuals have the capacity of transmitting the external form of the species unaltered to the offspring, and (2) not only a part but the whole of the protoplasm of any species possesses the specific constitution of that species.

It is of the greatest importance not only for the existence of the species, but also for the origin of new species, that the protoplasm, by reason of its specific constitution, should always take the same form. New species can only arise from those already in existence. This is equivalent to saying that the protoplasm of an existing species must undergo alterations in its constitution. Living protoplasm with new specific constitution must be produced from what already exists. How such a fundamental alteration is effected can only be guessed at by roundabout methods. One has to be content, as in so many other instances, with the results of experiment and experience, and with ascertaining, above everything, what influences are capable of altering the outward form of a whole or part of a plant either temporarily or permanently.

2.—ALTERATION IN THE FORM OF SPECIES.

Dependence of Plant Form on Soil and Climate.—Influence of Mutilation on the Form of Plants.—Alteration of Form by Parasitic Fungi.—Alteration of Form under the Influence of Gall-producing Insects.—Origin of New Forms by Crossing.

DEPENDENCE OF PLANT FORM ON SOIL AND CLIMATE.

The little town of Kitzbühel, in the North-east Tyrol, has a very remarkable position. On the north rises the Wilde or Vordere Kaiser, a limestone chain of mountains with steep, pale, furrowed sides, and on the south the Rettenstein group, a chain of dark slate mountains whose slopes are clothed far up with a green covering. The contrast presented by the landscape in its main features is also to be seen in the vegetation of these two mountain chains. On the limestone may be seen patches of turf composed of low stiff Sedges, Saxifrages whose formal rosettes and cushions overgrow the ledges and steps of the rugged limestone, the yellow-flowered Auricula, the Rock-rose-flowered Rhododendron, and white-flowered Cinquefoil adorning the gullies, dark groups of Mountain Pines bordered with bushes of Alpine Rose; and opposed to these, on the slate mountains, are carpets of thick turf composed of the Mat-grass sprinkled with Bell-flowers, *Arnica montana* and other Composites, groups of Alpine Alder and bushes of the rust-coloured Alpine Rose—these are contrasts in the plant-covering which would strike even a cursory observer, and would lead a naturalist to ask what could have been the cause. No wonder that the enthusiastic Botanist, Franz Unger, was fascinated by this remarkable phenomenon in the vegetable world. In his thirtieth year, furnished with a comprehensive scientific training, he came as a doctor to Kitzbühel, and with youthful ardour he used every hour of leisure from his professional duties in the investigation of the geological, climatic, and botanical conditions of his new locality, devoting his fullest attention to the relations between the plants and the rocks forming their substratum. The result of this study was his work, published in 1836, *On the Influence of Soil on the Distribution of Plants as shown in the Vegetation of the North-east Tyrol,* which marked an epoch in questions of this sort. The terminology introduced in the book found rapid entrance into the Botanical works of the time. Unger divided the plants of the district according to their occurrence on one or other of the substratums—in which lime and silica respectively predominated—into (1) those which grow and flourish on limestone only; (2) those which prefer limestone, but which will grow on other soils; (3) those which grow and flourish on silica only; and (4) those which, whilst preferring silica, will grow on other soils. He tabulated his results in such a way as to show clearly how certain species grew on the limestone and others on the silica-containing rock. Naturally these facts elicited a number of speculations. If the species *Gentiana Clusii, Hutchinsia alpina,* and *Juncus monanthos* growing on the limestone soil are replaced on the slaty soil by the similar (but yet distinct) species, *Gentiana acaulis* (*excisa*), *Hutchinsia brevicaulis,* and *Juncus trifidus,* we are justified in assuming that the difference in form is due to the influence of the substratum, *i.e.* to the influence of the chief materials in the rock—limestone and silica. But it has yet to be ascertained and proved, if possible by experiment, how this influence works; whether limestone and silica, respectively, introduce certain compounds into a plant, thus altering its outward appearance, or whether the difference is due rather to the fact that each plant-species requires so much lime or so much silica, and that when this is lacking in the soil the outward form becomes changed; or again, whether, after all, the physical properties of the substratum, its porosity, capacity for retaining water, and its specific heat, have not more influence on the form of plants than its chemical constitution.

Unger and his followers, amongst whom I enroll myself, thought they would obtain an answer to these questions by comparing the chemical composition of the plant-ash with that of the soil in which the plants were grown. But the results of careful investigations were anything but satisfactory. Both the substances named, the presence of which was supposed to be of special importance, could be demonstrated in most of the soils examined. Labrador felspar, hornblende, and other minerals in crystalline slate yield as much lime in the upper soil as is required by plants demanding or preferring limestone (classes 1 and 2, above), whilst the Limestones, which almost all contain clay, have silica enough for the needs of plants which demand or prefer silica (classes 3 and 4, above). Moreover, it was shown that plants have the power of obtaining materials which are valuable to them even when these occur around their roots in hardly appreciable quantity, so that they actually become accumulators of certain materials, and in this way a substance of which there are only minute traces in the underlying rock may be relatively abundant in the superficial layers of soil impregnated with the dead plant-remains (*cf.* vol. i. pp. 70 and 259).

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